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THE CENTRAL GUSTATORY PATHS IN THE BRAINS OF BONY FISHES.

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With Forty Figures in the Text.

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SECTION I. INTRODUCTION.

The conception of the nervous system as a mechanism for putting the organism into correspondence with the external environment and, in higher animals, for coordinating the reacting apparatus itself (internal environment) may be said to give the key to its evolutionary history. These two factors have given direction to the differentiation of the nervous system into somatic and visceral systems respectively and the further subdivision of each of these.

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[1] This study was awarded the Cartwright Prize for 1905 by the Alumni Association of the College of Physicians and Surgeons, Columbia University, New York. It is published simultaneously in the *Journal of Comparative Neurology and Psychology* and the *Bulletin of the Scientific Laboratories of Denison University*, pages 375 to 456 of volume XV of the *Journal* being severally identical with pages 35 to 116 of volume XIII of the *Bulletin*.

The labors of the students of nerve components have given us for the peripheral nervous system a paradigm or schema which seems to hold for all vertebrates, though with infinite variation in its details; and it now remains to correlate these peripheral components with the central conduction paths so as to give a detailed knowledge of the whole course of each reflex pathway.

In attacking this general problem there are obviously two general lines of procedure open to us:—(1) beginning with the simplest brains we may work out exhaustively for each critical species in the phylogenetic series the conduction paths as completely as possible by monographic treatment of types and thus in the end approximate to a reconstruction of the phyletic history of the nervous system. (2) Or we may take each sensori-motor reflex system as the unit and trace its phylogeny through the series of types. This second method has the obvious advantage that one can start with the system in question in some type where it attains maximum development and, having arrived at a thorough knowledge of its anatomy and physiology here, it will be easier to read this schema backwards to the more primitive animals, as well as forwards in its further evolutionary modifications. It is hardly necessary to call attention to the fact that the human nervous system is the least favorable starting point for this sort of a research except for the neo-pallium and its appendages.

Each method has its advantages. The monographic treatment of type brains is really far more difficult, even in the lowest vertebrates, because of the difficulty in interpreting such simple undifferentiated pictures and analyzing a complex where there are few salient features. But nature has effected the analysis for us in some of the more specialized types by the hypertrophy of isolated systems; and if, as sometimes happens, the other functional systems are in a primitive or reduced condition, we have a favorable point of approach for a monographic study of the exaggerated functional system (cf. JUDSON HERRICK, '03).

The purpose of this study is to make such a detailed analy-

sis of a single functional system of neurones—the gustatory system—in types where it reaches its maximum development and is obscured as little as possible by a high development of other systems. These conditions are fulfilled perfectly in the cyprinoid and siluroid fishes, whose brains are uncomplicated by any pathways leading to or from the cortex of the fore-brain and are in the main merely reflex mechanisms, but whose peripheral gustatory pathways are more highly developed than in any other vertebrates.

SECTION II. THE PERIPHERAL GUSTATORY SYSTEM IN FISHES.

As is well known, taste buds occur freely scattered over the mucous lining of the mouth and gills of nearly all fishes from the lips to the oesophagus. These are innervated by the VII, IX, and X cranial nerves. Similar taste buds, commonly called terminal buds, occur in the outer skin of some fishes and these also have been recently shown to be gustatory in function (JUDSON HERRICK, '04). They are, in all cases where the innervation is known, supplied by the facial nerve. All taste buds in the pharynx and back part of the mouth, then, are supplied from the vagus and glossopharyngeus, those in the front part of the mouth, lips and outer skin from a root of the facialis which apparently corresponds with the portio intermedia of human anatomy.

Associated with each of these roots are unspecialized visceral sensory fibers ending by free arborizations in the mucous membrane of the mouth cavity, these being very numerous in the region of the lower vagal roots and diminishing cephalad. The central connections of these two elements have not as yet been clearly differentiated, and both are provisionally designated the "communis system" of nerves by students of nerve components. With the unspecialized fibers we are not here concerned. The specialized communis fibers related with taste buds, either within or outside the mouth, and the ganglion cells from which they are derived will be termed the *peripheral gustatory system of neurones.*

The peripheral gustatory system has recently been worked up both anatomically and physiologically in a number of fishes, most thoroughly in the siluroids, or cat fishes (JUDSON HERRICK, '01 and '04). From the paper last cited we copy the accompanying figure (Fig. 1), which gives the peripheral distribution of the cutaneous branches of the communis root of the facial nerve to supply the taste buds in the outer skin, in the horned pout, Ameiurus.

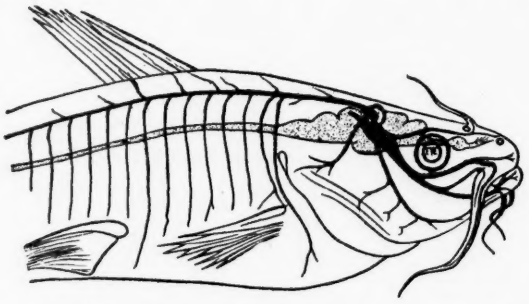

Fig. 1. A projection of the cutaneous branches of the communis root of the right facial nerve in *Ameiurus melas*, Jordan and Cope. Natural size.

The branches of this nerve which supply taste buds within the mouth are not drawn. All of the branches shown are gustatory in function. From the *Bulletin of the U. S. Fish Commission* for 1902 (JUDSON HERRICK, '04).

The general form of these buds of Ameiurus and their relations to the skin are shown in Figure 2. Practically all parts of the skin in these fishes are provided with taste buds supplied by this root, these same areas receiving also general cutaneous nerves for tactile sensation from other nerve roots, and the barblets being especially richly supplied with both sorts of nerve endings.

It has been determined by an experimental study of a series of both fresh water and marine fishes (JUDSON HERRICK, '04) that the cutaneous communis nerves are gustatory in function and that this function is absent from the skin in species where these nerves and their sense organs are not developed. When edible substances or sapid solutions were brought in contact with these cutaneous sense organs the fishes would react by the

appropriate movements to approach and seize the food and in the case of the horned pout, Ameiurus, it was found possible to differentiate a gustatory reaction from a tactile reaction and to prove that both senses possess a "local sign;" i. e., both the tactile and the gustatory reaction can be localized in space.

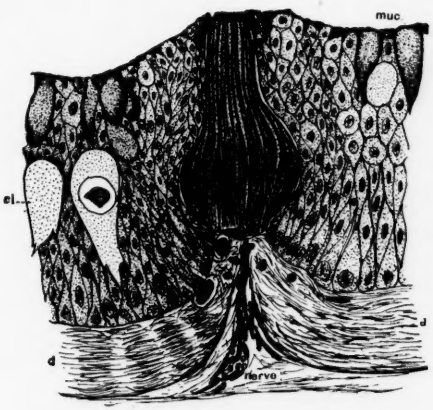

Fig. 2. Section through the skin of the top of the head of *Amiurus melas*, showing a terminal bud. From the *Journal of Comparative Neurology*. (JUDSON HERRICK, '01).

At *d* is the dermis which is raised into a low papilla under the sense organ and whose center is pierced by the nerve for the organ; *cl.*, clavate cells of LEYDIG; *muc.*, mucus cells of the epidermis.

The peripheral pathways for these motor responses are now well known and the problem of the present research may be thus stated: Given the terminal relations of the peripheral gustatory neurones and the peripheral motor neurones involved in the known gustatory reflex movements of these fishes, what are the central connections between them?

Experiment has shown that the taste buds in the outer skin function in substantially the same way as those within the mouth, though there are certain obvious differences, particularly the fact that the stimulus if applied to the cutaneous taste buds

usually calls forth a movement of the whole body toward the food object, while this is unnecessary in the case of a gustatory stimulus received within the mouth. This is the probable reason for the differentiation of a special center in the medulla oblongata for the reception of the facial root of the communis system, the lobus facialis, or "tuberculum impar," in those species which possess large numbers of terminal buds in the outer skin.

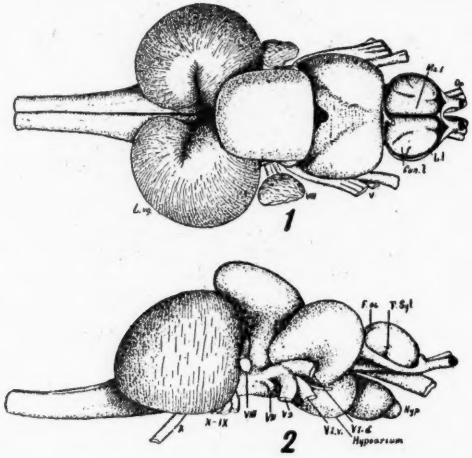

Fig. 3. Two views of the brain of the buffalo fish, *Carpiodes velifer* (Raf.), (1) from above, (2) from the right side. × 2. After C. L. HERRICK.

The vagal lobes (*L. vg.*) are relatively larger than in the carp and, with the overhanging cerebellum, completely conceal the facial lobe. In the lower figure the branches of the trigemino-facial root complex are marked *V1.d.*, *V1.v.*, *V2*, *VII*, and the root of the auditory nerve *VIII*. Between the latter and the caudal tip of the optic lobe is a well-defined protuberance ventrally of the cerebellum. This is the lateral portion of the superior secondary gustatory nucleus (*Rindenknoten*, MAYSER). Caudad of this, immediately dorsally of the VIII root, is the small lobus lineae lateralis (JOHNSTON) from which the tuberculum acusticum and cerebellar crest extend caudad beneath the vagal lobe. In the upper figure, the median shaded part of the roof of the optocoele is membranous, the optic lobes being widely divaricated by the enormous valvula cerebelli. In both figures the membranous roof of the fore-brain is dissected away to show the lobules of the basal ganglia, and the olfactory bulbs are cut away.

With the exception just noted, it is probably safe to assume that there will be found broad lines of similarity between

both the peripheral and the central gustatory paths in all vertebrate types and that fishes like the carp with enormous hypertrophy of the gustatory roots of the VII, IX and X nerves may safely be used as guides to point the way for further researches upon the gustatory paths of higher vertebrates where the system is less easily analyzed. Such being the case, our problem assumes a measure of importance when we remember that the central gustatory pathway is at present almost totally unknown in all vertebrates, including man, and that even the peripheral pathway is still in dispute among students of human anatomy.

It has been already pointed out (JUDSON HERRICK, '04) that the siluroids (cat fishes and horned pouts) and the larger cyprinoids (carps, suckers, etc.) present a striking similarity to each other and contrast to other teleosts in both the peripheral and the central nervous systems, and that these features center about the gustatory pathways. In teleosts generally the gustatory pathway from the lining of the mouth in the branchial region, entering the brain by the communis roots of the IX and X nerves, and the gustatory pathway from the anterior part of the mouth and from the outer skin, entering by the communis VII root, terminate together in a single cerebral enlargement, the lobus vagi. But in these two groups of fishes we have a second tuberosity, as mentioned above, developed for the communis root of the facialis to provide for the unusually large number of taste buds in the outer skin supplied by this nerve.

In the cyprinoids, particularly the carp-like forms, both of these lobes are enlarged, correlated with a high development of the taste buds in each of the corresponding peripheral regions, but particularly in the vagal region to supply the remarkable collection of taste buds on the palatal organ. In the siluroids, on the other hand, there is no hypertrophy of the gustatory organs in the branchial region and the vagal lobes, accordingly, are essentially similar to those of other teleosts. But the highly developed cutaneous gustatory organs innervated by the facialis have called forth an enlargement of the facial lobe greater than that of cyprinoids. Since in the siluroids all of the taste buds of the outer skin are supplied by the communis root of the

facialis (JUDSON HERRICK, '01) and since the palatal and other branches of the communis VII root which supply taste buds within the mouth are not enlarged, as compared with other fishes, it is clear that the enormous communis VII root and the lobus facialis in which it terminates are related mainly to cutaneous taste buds in these fishes.

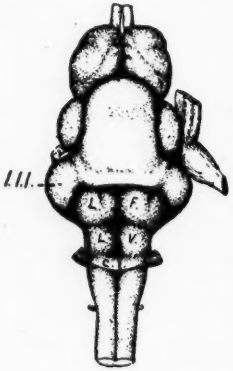

Fig. 4. Dorsal view of the brain of the yellow cat fish, *Leptops olivaris* (Raf.), × 2.

The olfactory bulbs are cut off; also the membranous roof of the fourth ventricle, exposing the facial lobes (*L. F.*) and vagal lobes (*L. V.*). This ventricle is bounded behind by a transverse ridge containing the commissura infima HALLERI (*c. i.*) and the commissural nucleus of CAJAL. The tuberosity laterally of the cerebellum and facial lobe is the lobus lineae lateralis (*l. l. l.*), which is greatly enlarged and entirely conceals the superior secondary gustatory nucleus.

SECTION III. THE CENTRAL GUSTATORY SYSTEM OF CYPRINOID FISHES.

We shall now proceed with a description of the gustatory pathways in a selected series of teleosts, beginning with the larger cyprinoids where it attains its maximum development. The results here obtained will be controlled by an equally careful examination of the brains of siluroid fishes (particularly Ameiurus), whose gustatory centers differ greatly in detail from those of the carp-like forms. These minor differences will serve to bring out more clearly the points of fundamental resemblance, which are very striking.

The end-station of the gustatory neurones of the first order (peripheral neurones) is the nucleus of origin for the neurones of the second order, giving rise to secondary gustatory tracts, and these in turn to tertiary tracts. The nomenclature of these tracts and centers offers almost insuperable difficulties and some new terms will have to be introduced and old ones more nar-

rowly defined. A summary of the nomenclature here employed for the gustatory system of these fishes is given in tabular form in Section V, to which frequent reference should be made.

1. Primary Gustatory Centers.

The general topography for the vagal and facial lobes of cyprinoid fishes has often been described, and the reader is referred for the details to the classic paper of MAYSER ('82), and also to the figures of BELA HALLER ('96), whose descriptions, however, I do not in all things confirm. I have found little in the extensive work of this author ('98) on the brains of Salmo and Scyllium which sheds further light on the secondary connections of the vagal lobe. However, I do not profess to have mastered the contents of this unsystematic and obscure paper, though I have dilligently studied it. Nor is there anything of importance from our present point of view in the recent dissertation on the vagal lobes of cyprinoids by GROTH ('00), whose purpose was merely to test the accuracy of some of HALLER's observations on nerve anastomoses in these fishes.

The vagal lobe of the cyprinoids, as compared with that of the siluroids and the teleosts generally, represents an enlargement of both the sensory and the motor centers of the vagus and glossopharyngeus. This enlargement is correlated with the development of the curious palatal organ in the mouth of these fishes, the sensory fibers being derived from the taste buds which cover the surface of this organ and the motor fibers going out chiefly to the small muscles which permeate its interior. The "motor layer" of the vagal lobe, from which these motor fibers are derived is a dorsal extension of the nucleus ambiguus. The latter nucleus has the typical position and relations, supplying the branchial musculature, and is not commonly regarded as a part of the vagal lobe.

We shall describe, so far as the material at command permits, the conduction pathways in the vagal lobe of the larger cyprinoids on the basis of sections of adult and young brains cut in various planes and stained by DELAFIELD's haematoxylin and the methods of WEIGERT-PAL and GOLGI. The illustrations

given throughout the remainder of this paper are all camera drawings of single sections, except Fig. 20, which is a composite, and the schemata, Figs. 38, 39 and 40.

First a few words by way of general orientation. The vagal and facial lobes are dorsal structures in the oblongata, but they do *not* represent, as commonly taught, the morphological continuation of the dorsal horns of the spinal cord. These are represented in the spinal V tract and its associated substantia gelatinosa Rolandi, their ventro-lateral position in the vagus region of these brains being due to crowding by the more mesially placed gustatory centers. The latter centers, therefore, if morphologically related to anything in the spinal cord, must represent spinal structures lying dorsally of the canalis centralis and beneath the floor of the dorsal fissure. In the oblongata this fissure opens out and its floor becomes greatly extended to form the membranous roof plate (His), or velum medullare posterior, *beneath* which the lobes in question are developed (cf. Judson Herrick, '99, p. 213).

Figure 5, taken midway of the vagal and facial lobes of the carp, illustrates how these structures are superposed upon the great longitudinal conduction paths which constitute the chief landmarks of morphological relationship. The spinal V tract, whose substantia gelatinosa at this level is reduced to a mere vestige, lies ventrally of both the sensory and motor vagus roots. Crowded into the space ordinarily occupied by the substantia gelatinosa Rolandi are the great longitudinal secondary gustatory paths, ascending and descending. Mesially of these is the substantia reticularis, shown by Cajal and others to be the continuation of the ventro-lateral funicle of the spinal cord and to be composed of short paths, mostly sensory fibers of the

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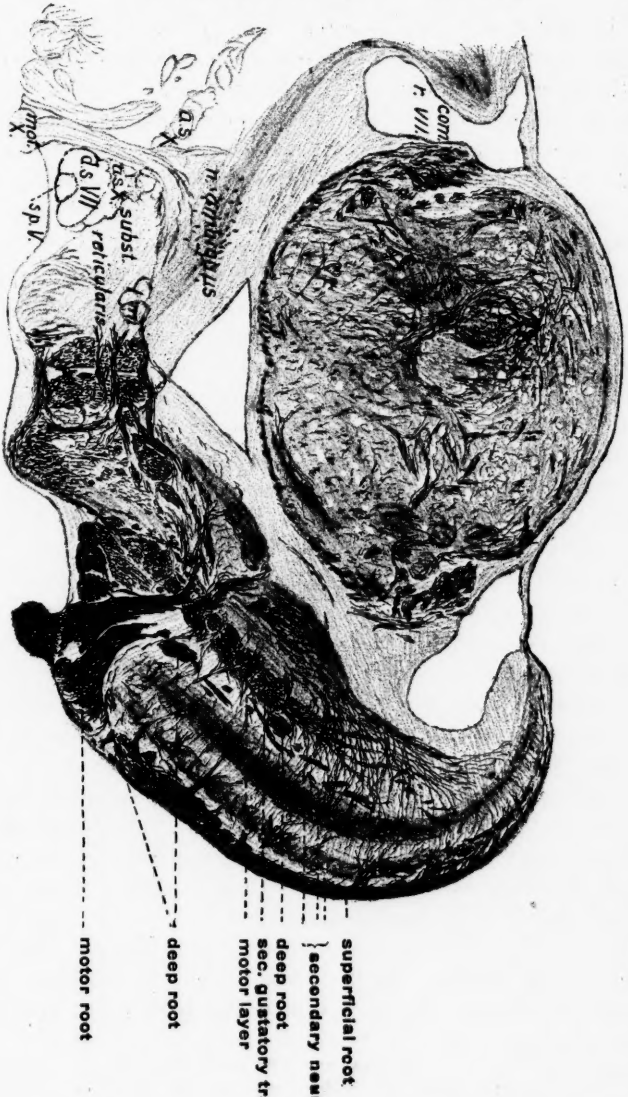
Fig. 5. A transverse section taken through the middle of the vagal and facial lobes of an adult carp stained by the method of Weigert-Pal. × 16.

The layers of the facial lobes and the vagus roots are designated at the right. *a. s. X.*, ascending secondary gustatory tract from the vagal lobe; *com. r. VII*, communis (gustatory) root of the facialis entering the facial lobe; *d. s. VII*, descending secondary gustatory tract from the facial lobe; *lm.*, lemniscus (laterales Längsbündel, Mayser); *sp. V.* spinal root of the trigeminus.


r. VII
com.
n. ampullaris
d.s.X
d.s.VII
t.s.X subst. reticularis
sp.V.
motor X.
superficial root
secondary neurones
deep root
sec. gustatory tract
motor layer
deep root
motor root

third order designed to distribute sensory excitations over a large field of motor nuclei of the oblongata. Close to the raphé in the median line is the fasciculus longitudinalis medialis, likewise composed largely of short paths and chiefly motor. Between this fasciculus and the substantia reticularis, there is ventrally the continuation of the ventral funicle of the spinal cord and dorsally the lemniscus (funiculus lateralis, FRITSCH; laterales Längsbündel, STIEDA and MAYSER).

The *lemniscus* is very complex. It clearly is composed in the main of crossed ascending fibers from the primary sensory centers of the spinal cord and oblongata to the mid-brain. These fibers correspond closely with the lemniscus lateralis or lateral fillet of mammals. The lemniscus medialis, or direct pathway to the cerebral cortex, as found in mammals, is of course not present here and this whole ascending path I shall term simply lemniscus. It probably receives fibers from the whole length of the spinal cord with a large accession of similar fibers from the funicular nuclei and enormous numbers of fibers from the tuberculum acusticum. It receives no appreciable number of fibers from the vagal lobes or other visceral sensory centers and therefore may be considered a somatic sensory secondary tract. It terminates in the mid-brain beneath the tectum in the protuberance into the optocoele which is so characteristic of the teleosts and is termed the torus semicircularis (nucleus lateralis mesencephali, EDINGER). This body, in fact, seems to be primarily the end-nucleus of this tract. Whether this bundle also contains descending fibers I do not know, but am sure that if present they are relatively few in teleosts. Such descending fibers would of course have to be excluded from the designation lemniscus.[1]

Some of the smaller cyprinoids (e. g., Notropis) exhibit but little enlargement of the vagal lobes. In the gold fish (*Carassius auratus*) the vagal lobe is greatly enlarged, but the

[1] The reader will note that this tract is designated *lemniscus* on account of its partial homology with the tract of that name in the mammals, and that it has nothing to do with the so-called lemniscus of MAYSER and others, or tractus tectobulbaris et spinalis.

sensory roots of the IX and X nerves penetrate at once to its deeper layers and then turn outward to end near the surface much as will be described in Ameiurus. In Cycleptus the lobe is larger and the sensory roots penetrate but little before they spread out to end in a superficial layer of large cells which stain very pale in haematoxylin. And in the carp (Fig. 5), whose vagal lobes are still more enlarged, the greater part of the sensory roots do not penetrate, but spread out over the whole outer surface of the lobe (constituting MAYSER'S first layer), thence to pass in separate strands directly into a thick layer exhibiting alternate bands of crowded small cells and dense neuropil (MAYSER'S second layer).

This will be termed the *layer of secondary neurones.* Sections stained by DELAFIELD'S haematoxylin show within it seven concentric bands of cells and neuropil which are more or less sharply distinguishable, of which the two outer are of greatest importance. The first is a thin layer of crowded cells of relatively large size which take up a very pale stain—the chief secondary gustatory neurones. Immediately internal to and among these cells are smaller very closely crowded cells whose nuclei take up a very intense stain. These will be termed the smaller gustatory neurones. The other bands contain chiefly minute cells with deeply staining nuclei and occasionally larger, irregularly shaped cells among them, while the inner border of this layer is a band of neuropil containing a few large cells which take a very pale stain. Sections stained by the method of PAL show sensory root fibers entering this band at its inner border. These root fibers will be termed the deep communis root of the vagus, as distinguished from the larger superficial root (Fig. 5). The fibers of the deep root turn outward to end in the second layer along with those of the superficial root.

This layer of secondary neurones is very wide in Cyprinus and is traversed radially by unmedullated and delicately medullated fibers for the deeper layers of the vagal lobe. The large pale cells forming its outer boundary are the most important and characteristic cells of the lobe, for they give rise to the

great secondary gustatory tracts which leave the lobe for distant centers. The narrow layer of smaller cells adjacent to these may share this function, but their neurites are mostly shorter. The small cells of the other bands of this layer have short neurites which terminate for the most part within the lobe and are therefore called intrinsic secondary gustatory neurones.

Immediately internal to the seventh band of the layer of secondary neurones is MAYSER's third layer, the *layer of secondary gustatory fibers*, which pass ventrally to constitute the "secondary vagus bundle" of MAYSER. These fibers are of small caliber with thin sheaths which take a very pale stain by the WEIGERT method.

Internally from the secondary gustatory tract is the *motor layer* (MAYSER's fourth), containing large cells which give rise to motor root fibers of the IX and X nerves. The thick ependyma containing large blood vessels is MAYSER's fifth layer. Some of its supporting elements are shown in Fig. 6.

The endings of the peripheral neurones which compose the superficial layer of root fibers of the vagal lobe of the cyprinoids are richly impregnated in many of my GOLGI preparations. Those of the deeper layers impregnate with much more difficulty. They are seen in Fig. 6. The superficial fibers end by extensive terminal arborizations which ramify widely among the dendrites of the chief secondary gustatory neurones, forming a very dense neuropil in the more superficial parts of the layer of secondary neurones, though some penetrate through the whole thickness of this layer. These endings are shown in Figs. 6 and 15 and somewhat imperfectly in Fig. 8. Fig. 6 shows that the slender strands of root fibers pass from the superficial to the deep layers of root fibers throughout the whole extent of the vagal lobe.

The most caudal fibers of the vagus constitute the descending or spinal root of this nerve, which passes a very short distance caudad to terminate in the grey centers associated with the commissura infima HALLERI and funicular nuclei as CAJAL ('96, p. 46) describes the endings of the fasciculus solitarius in the nucleus commissurale of the mouse.

The general arrangement of the *chief secondary neurones* may be understood by reference to Fig. 7, drawn from a sagittal section of a young carp, where these cells are richly impreg-

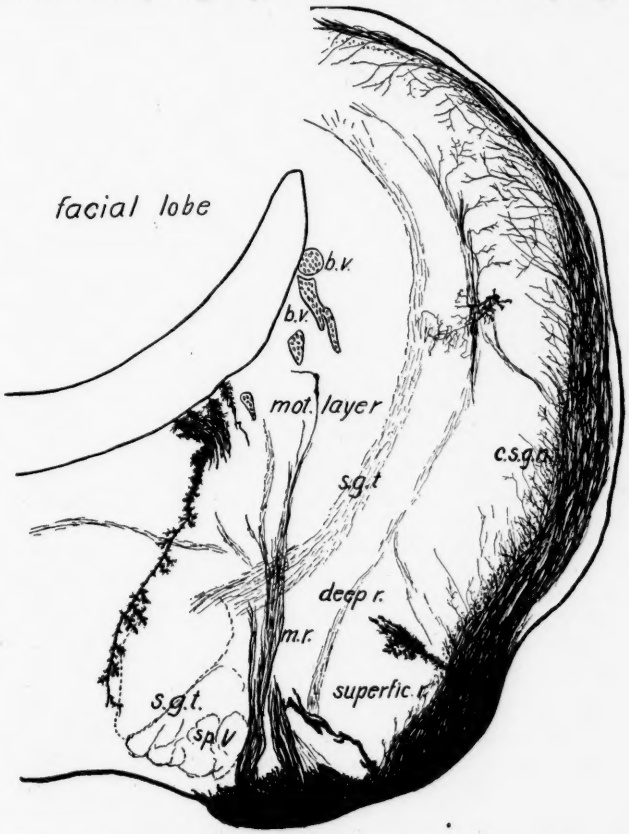


Fig. 6. Transection through the vagal lobe of *Catastomus commersoni.* GOLGI method. × 40.

The section illustrates the endings of the superficial and deep layers of root fibers of the vagus and the position of the chief secondary gustatory neurones (*c.s.g.n.*). An intrinsic neurone of type II is shown with dendrites in relation with the termini of the deep root. Two neuroglia cells of the superficial series are drawn and several of the deeper series (some of the latter having been drawn from an adjacent section). *b.v.*, blood vessel; *m.r.*, motor root of the vagus; *s.g.t.*, secondary gustatory tract; *sp.V*, spinal V tract.

nated. The layer of root fibers is not impregnated in this preparation, but its relations are suggested in Fig. 8 and more clearly in Fig. 6. In Fig. 8 root fibers are stained in the ventral part

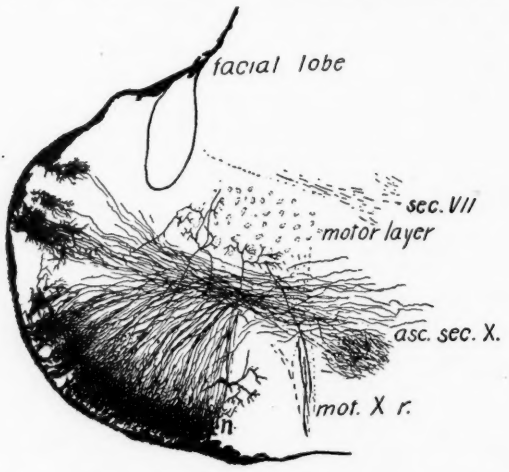


Fig 7. Section through the vagal lobe of a young carp, 5 cm. long. GOLGI method. × 40.

The section is approximately sagittal, but strongly inclined so that, while the caudal end (at the left of the figure) is near the median line, forward it passes toward the right. It includes, therefore, the motor nucleus of the right vagal lobe and the right side of the facial lobe, only the extreme caudo-ventral border of which is indicated. The preparation gives a typical view of the chief secondary gustatory neurones of the vagal lobe. One of the smaller secondary neurones (*n*) is shown at the extreme ventral (lower) side of the vagal lobe (cf. Fig. 11). A few scattered neurones of the deeper portions of the layer of secondary neurones are imperfectly impregnated. A few thick fibers are seen to pass from the layer of secondary neurones into the motor layer to arborize widely among its cells. Their origin could not be determined, but is probably from some of the deeper cells of the layer of secondary neurones. *Asc. sec. X.*, ascending secondary gustatory tract; *mot. X r.*, motor root of the vagus.

of the vagal lobe, but only secondary neurones in its dorsal part. In preparations where both are impregnated together the peripheral layer of secondary neurones presents an indescribably intricate complex of interlacing fibers. Fig. 9 shows a single one of the chief secondary neurones of Fig. 8 drawn separately on a larger scale.

These neurones are densely crowded in radial arrangement over the entire periphery of the vagal lobe and are of very peculiar form. They are unipolar with irregularly elongated cell body and dendrite springing from the inner end. The

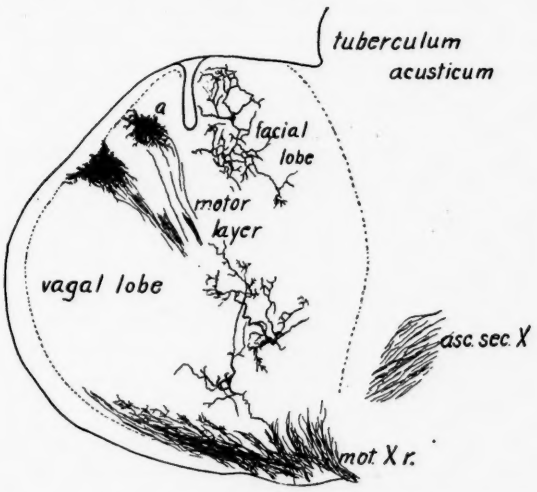


Fig. 8. Sagittal section through the vagal lobe of a young carp. GOLGI method. Drawn from the same series as Fig. 7, but farther toward the right side, so as to cut tangentially the extreme right borders of the vagal and facial lobes. × 40.

The figure illustrates a few gustatory neurones of the vagal lobe and (imperfectly) endings of the gustatory root fibers, also two neurones of the deeper portion of the layer of secondary neurones whose processes reach the motor layer (cf. Fig. 7). These cells appear to be of the same type as the large cell lying in the layer of secondary tracts in Fig. 13. The neurone in the facial lobe is sketched in from the section lying next mesially, It occupies the area intermedia of the facial lobe and spreads out over the whole of the lateral aspect of the latter, its neurite not being shown. It is evidently of the same type as the one figured in Fig 18 at *a*.

peripheral end of the cell body is drawn out to a point which seems usually to reach the external limiting membrane of the vagal lobe. In these young fishes the external layer of root fibers is relatively thin. In older carp this layer is much thicker and there is no well defined external limiting membrane. The bushy dendrite breaks up at once into a very dense mass of

exceedingly fine branchlets among which the arborizations of the root fibers end. From one or more of the terminal branches of this dendrite a very delicate neurite arises and goes by the shortest path directly into the layer of secondary tracts by which it leaves the vagal lobe to enter the longitudinal secondary gustatory tracts of the oblongata, meanwhile taking up a

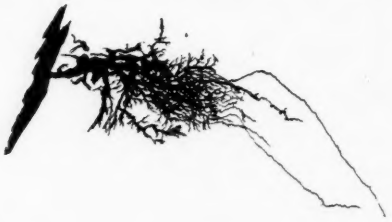


Fig. 9. A chief secondary gustatory neurone from the vagal lobe of the carp—the neurone designated *a* on Fig. 8. × 250. The black mass at the left of the neurone is precipitate deposited in the external limitating membrane of the vagal lobe.

very delicate medullary sheath. In its passage through the layer of secondary tracts it sometimes gives collaterals into the motor layer of the vagal lobe (Fig. 10).

Upon casual examination these chief neurones might suggest the appearance of neuroglia elements. The latter, however, are of totally different form (Fig. 6) and there is no opportunity for confusion. The gustatory neurones have exceedingly fine and densely branched dendrites, while the branches of the neuroglia are thicker and of the peculiar mossy or pulverulent appearance so characteristic of the supporting elements. The neuroglia, moreover, as a rule impregnates with a dark brown instead of black color.

Besides the chief gustatory neurones just described, there are closely associated with them just internally the smaller gustatory neurones shown in Figs. 11 and 12. These have the same general form and arrangement, but are much simpler. The cell body is smaller and usually rounded and the dendrite less profusely branched. The slender neurite arises from the tip of the dendrite and enters the layer of secondary tracts.

Some of these fibers or their collaterals enter directly the motor layer and there arborize. Others end by simple arborizations in the substantia reticularis and others turn caudad in the descending secondary communis tract. Whether any go cephalad

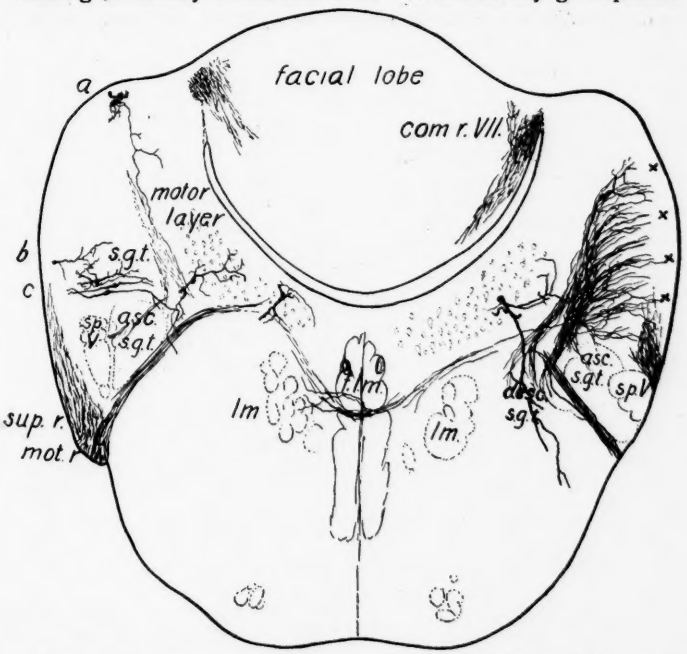


Fig. 10. Transverse section through the vagal and facial lobes of the spotted sucker, *Minytrema melanops* (Raf.) from a fish 8 cm. long. GOLGI method. × 40.

On the left at *a* a single chief secondary gustatory neurone is impregnated whose neurite sends collaterals into the dorsal part of the motor layer of the vagal lobe. On the right the area marked by the crosses is filled with a rich impregnation of similar cells which are not sketched in. At *b* is a single secondary neurone of the type shown in Fig. 12, and at *c* imperfect impregnations of deeper secondary neurones of the intrinsic type. On the right one cell of the motor layer is impregnated whose dendrites reach secondary gustatory tracts partly within the vagal lobe and partly in the substantia reticularis.

asc.s.g.t., ascending gustatory tract; *com.r.VII*, communis (gustatory) root of the facialis; *desc.s.g.t.*, descending secondary gustatory tract, entering substantia reticularis; *f.l.m.*, fasciculus longitudinalis medialis; *lm.*, lemniscus; *mot.r.*, motor root of the vagus; *s.g.t.*, secondary gustatory tract from the vagal lobe; *sp.V*, spinal V tract; *sup.r.*, superficial gustatory root of the vagus.

in the ascending secondary tract I have not determined.

These neurones clearly are of the same type as the chief gustatory neurones, but their neurites have a shorter course as a rule. Cells of this type in my preparations are impregnated chiefly in the more superficial parts of the layer of sec-

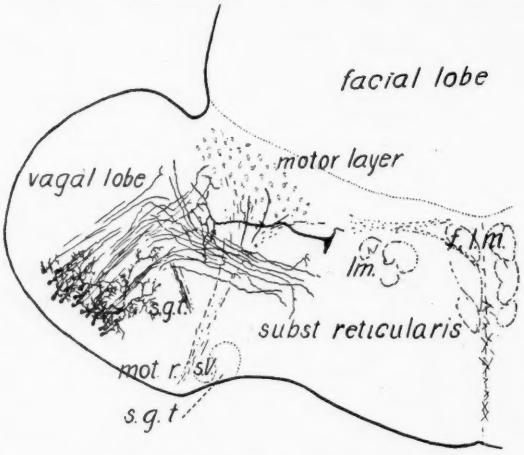


Fig. 11. Transverse section through the vagal and facial lobes of a young carp 5 cm. long. The section is obliquely inclined with the left side a little farther caudad than the right and the dorsal side much farther cephalad than the ventral. GOLGI method. × 40.

The section passes through the extreme cephalic end of the vagal lobe. None of the chief gustatory neurones are impregnated in this preparation, the superficial cells drawn being of the smaller variety. Among them are two intrinsic neurones of the vagal lobe. There is impregnated also a single large neurone in the dorsal part of the substantia reticularis one of whose dendrites reaches the layer of secondary gustatory tracts and whose neurite passes toward the ventral commissure.

f.l.m., fasciculus longitudinalis medialis; *lm.*, lemniscus; *mot.r.*, motor root of the vagus; *s.g.t.*, secondary gustatory tract; *s. V*, spinal V tract.

ondary neurones; but sections stained with haematoxylin show very numerous nuclei of the same appearance throughout this layer and occasional GOLGI impregnations show that they are in fact scattered less freely throughout the thickness of the layer.

There are frequent impregnations, usually very imperfect, of larger cells of different kinds in the deeper parts of this layer,

as shown in Figs. 7, 8, 10 and 13; but I have not been able to trace the connections of all these types of cells. There are many indications that they reach the motor layer of the vagal lobe (Fig. 14) and substantia reticularis of the oblongata immediately below the vagal lobe. In most of these cases the dendrites spread irregularly among the other cells of this layer

Fig. 12. A single neurone of the smaller gustatory type from the right vagal lobe of the carp. Drawn from the same series as Fig. 11, two sections farther caudad. GOLGI method. × 250.

The main axis of the dendrite is directly prolonged to form the neurite. Terminal arborizations of the gustatory root fibers occur among these dendrites. The broken line represents the outer border of the vagal lobe.

and the processes which penetrate the motor layer do not differ essentially from the others. There is one type of cells, however, among these whose dendrites extend tangentially over a very wide area (Fig. 16, *b* and Fig. 18, *b*). In one case (Fig. 13) a neurite from a cell was seen to enter the secondary gustatory tract; but its further course is unknown. Fig. 13 also shows one of the smallest of these intrinsic cells whose thorny dendrites are sharply contrasted to the very delicate much branched neurite (neuropodium), giving the cell the characteristic form of GOLGI's type II.

This is apparently the most frequent type of these intrinsic cells, though the neurite is rarely impregnated in recognizable form. Fig. 6 illustrates a different form of this type of cell, with cell body and dendrites among the endings of the deep layer of root fibers and neuropodium between this layer and the layer of secondary tracts.

STANNIUS ('49, p. 82) has shown that mechanical stimulation of the vagal lobe of the carp produces movements of the intrinsic muscles of the palatal organ. Since the nucleus ambiguus of the cyprinoids does not differ from that of other

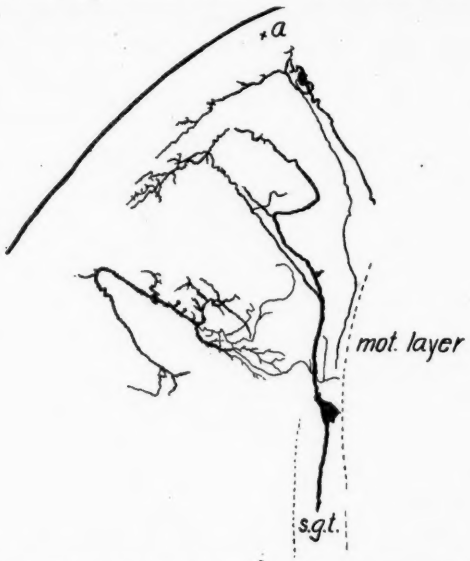


Fig. 13. Portion of the vagal lobe from a transverse section of the brain of *Minytrema melanops* (Raf.) 8 cm. long. GOLGI method. × 187.

This is drawn from the same series as Fig. 10, the sections being adjacent. For ease of orientation the position of the neurone marked *a* on Fig. 10 is designated *a* in this sketch. The large neurone at the bottom of the figure in the layer of secondary gustatory tracts sends one of its two chief dendrites outward into relation with the arborizations of the peripheral gustatory neurones, the other is cut off. The neurite is not shown. The intrinsic neurone to the left of it is a characteristic type II cell. The intrinsic neurone at the top of the figure is drawn in from the adjacent section. Its neurite enters the secondary gustatory tract (*s.g.t.*)

teleosts, in which it is known to innervate the branchial musculature, it is extremely probable that the cells of the motor layer of the vagal lobe give rise to the nerve fibers for these intrinsic muscles, for these two structures (the palatal organ and motor layer of the vagal lobe) are always developed proportionately with each other.

WEIGERT sections show very clearly that fibers of the motor roots of the vagus and glossopharyngeus arise not only from the nucleus ambiguus but also from the motor layer of the vagal lobe, as has been well known since MAYSER.

My GOLGI preparations very rarely show good impregnations either of the cells of the motor layer or of the nucleus ambiguus. The latter have the form and arrangement which have been often figured, the main dendrites spreading out in the substantia reticularis and reaching the extreme ventro-lateral border of the oblongata. Other smaller dendrites spread out within the nucleus itself and the neurite usually springs from the base of the main dendrite. The dendrites of the cells of the motor layer in some cases spread out within this layer, where they come into relation with the radial fibers which enter it from the layer of secondary neurones. Others reach out into the layer of secondary tracts and into the substantia reticularis (Fig 10), in both of which places they reach collaterals from the secondary gustatory tracts.

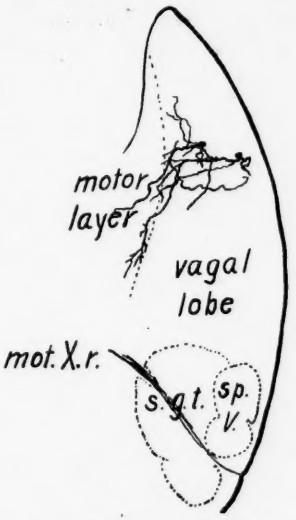


Fig. 14. Transverse section of the vagal lobe of the right side of a young carp, 5 cm. long. GOLGI method. × 50.

Illustrating two intrinsic secondary neurones of the vagal lobe whose processes extend inward to reach the motor layer. *s.g.t.*, secondary gustatory tract; *sp. V*, spinal V tract.

It appears that in no case do the peripheral motor neurones come into direct relation with the peripheral gustatory neurones, but at least one intermediary element is always interposed. These elements may be the intrinsic neurones of the vagal lobe, for short reflex arcs, or the chief secondary gustatory neurones for more complex reflex connections reaching beyond the vagal region of the brain.

The substantia reticularis is clearly the chief medium of communication between the sensory and motor centers for simple reflex paths here, as in higher vertebrates. This reticular substance receives gustatory fibers both from the secondary gustatory tracts and from the intrinsic neurones of the vagal lobe. We shall see beyond that it also receives fibers from the facial lobe.

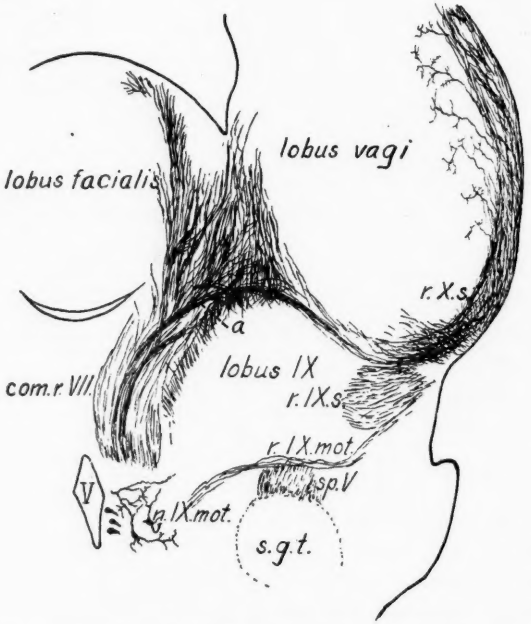


Fig. 15. Section through the right lobus glossopharyngei of a young carp 8 cm. long. GOLGI method. × 40.

The section is approximately transverse, but very oblique, so that the right side and the ventral surface are much farther cephalad. It cuts the lobus IX at its widest part and shows a strand of the communis root of the facialis (*a*) arching over its dorsal side and apparently entering both this lobe and the cephalic part of the lobus vagi. Terminal arborizations of the communis root of the vagus are also shown ending in the layer of secondary neurones of the lobus vagi.

com.r.VII, communis (gustatory) root of the facialis; *n.IX.mot.*, motor nucleus of the IX nerve; *r.IX.mot.*, motor root of the IX nerve; *r.IX.s.*, sensory root of the IX nerve; *r.X.s.*, superficial gustatory vagus root; *s.g.t.*, secondary gustatory tract; *sp.V*, spinal V tract; *V*, ventricle.

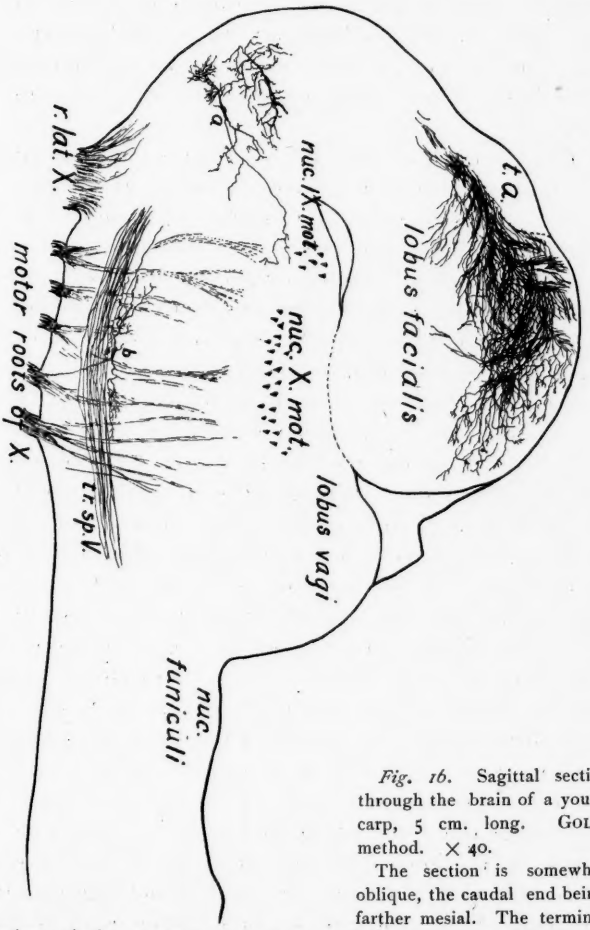


Fig. 16. Sagittal section through the brain of a young carp, 5 cm. long. GOLGI method. × 40.

The section is somewhat oblique, the caudal end being farther mesial. The terminal arborizations of the gustatory root of the facial nerve are richly impregnated. Two neurones are shown in the extreme cephalic part of the lobus IX, one of whose neurites (*a*) arborizes in the motor IX nucleus. These neurones lie in about the transverse level indicated in Fig. 17 and at the level of *r. IX. sen.* in Fig. 18. Their dendrites are reached by gustatory root fibers of the IX nerve. The neurone marked *b* is evidently of the same type as the one similarly designated in Fig. 18. *r. lat. X.*, ramus lateralis vagi; *t. a.*, caudal tip of tuberculum acusticum; *tr. sp. V.*, spinal V root.

Before proceeding with the description of the long secondary gustatory tracts from the vagal lobe we shall describe the internal structures of the glossopharyngeal and facial lobes, as the long tracts from all these centers can best be described together.

Between the vagal and the facial lobes of cyprinoids is a small tuberosity which, as pointed out by B. HALLER ('96, p. 93 and Fig. 12), receives the glossopharyngeus nerve. It may be termed the *lobus glossopharyngei.* It is very distinct in forms like the gold-fish, Carassius, whose glossopharyngeus nerves are far separated from the vagus, the sensory IX nerve entering its dorsal side and the motor IX its ventral. It appears in the carp at a level somewhat cephalad of that shown in Fig. 5 along the line of union of the vagal and facial lobes. In this type it appears to receive from behind some fibers from the vagus roots; at any rate the IX and X roots are somewhat confused in this region. In both the carp and the gold-fish it receives from in front filaments of the communis root of the facialis. These filaments are very clearly shown arching over the dorsal side of the lobus IX in an oblique GOLGI section (Fig. 15, *a*); a certain part of the facial root apparently also reaches the cephalic end of the lobus vagi. It would be interesting to learn whether these facial fibers which separate from the facial lobe to end in connection with gustatory fibers from the mouth cavity coming in by the IX and X nerves are derived from the palatine and other facial branches which also supply taste buds within the mouth.

The lobus glossopharyngei has essentially the same connections as the lobus vagi. Fig. 16 gives an impregnation of two of the intrinsic neurones of the extreme cephalic part of the lobus IX in sagittal section of the brain of a young carp. The sensory (gustatory) fibers of the IX nerve end among the dendrites of these neurones. The neurone at the extreme left does not show its neurite, but the neurite of the one marked *a* is shown completely, arborizing in the motor IX nucleus, thus completing the simplest gustatory reflex arc for the IX nerve.

The structure of the *facial lobe* (tuberculum impar, "lobus

trigemini," MAYSER) of the carp is considerably simpler than that of the vagal lobes. It is in general similar in internal organization to the facial lobes of Ameiurus, though its cells are of quite different form and it differs externally in that there is a complete fusion in the middle line of the right and left lobes with no clearly defined external or internal boundary between them.

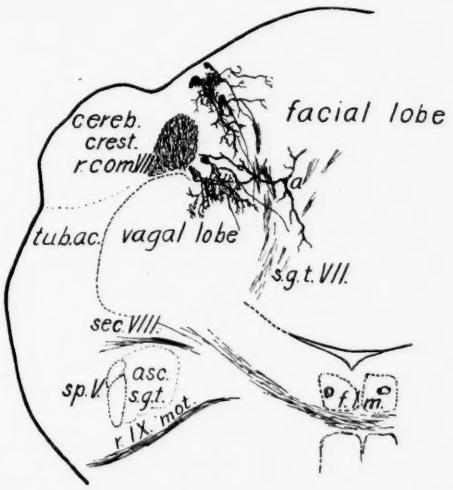


Fig. 17. Transverse section through the facial lobe of *Minytrema melanops* (Raf.). GOLGI method. × 40.

The section passes through the cephalic part of the facial lobe and includes the extreme cephalic end of the vagal lobe and the caudal end of the tuberculum acusticum. It shows five chief secondary gustatory neurones at the surface of the lobe and internally at *a* an imperfect impregnation of a cell of the intermediate zone of the same type shown in Fig. 18, *a*.

asc.s.g.t., main ascending secondary gustatory tract; *f.l.m.*, fasciculus longitudinalis medialis; *r.com. VII*, communis (gustatory) root of the facialis; *r.IX. mot.*, motor root of the glossopharyngeus; *sec. VIII*, secondary fibers from the tuberculum acusticum to ventral commissure; *s.g.t. VII*, secondary gustatory tract from the facial lobe; *sp. V*, spinal V tract; *tub.ac.*, tuberculum acusticum.

The center of the lobe is filled with very small intrinsic neurones arranged in dense clusters or rosettes of from 10 to 100 cells each. In Fig. 5 the clear spaces in the neuropil of the

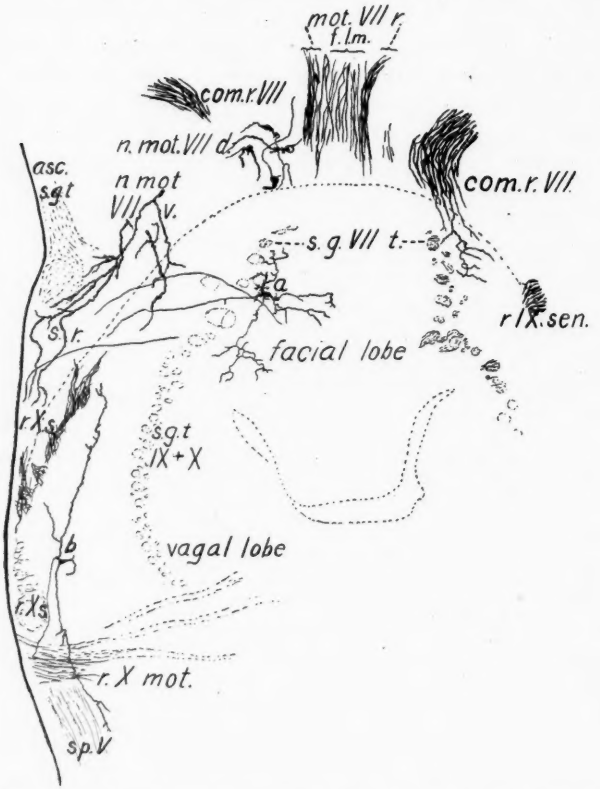


Fig. 18. Horizontal section through the base of the vagal and facial lobes of *Minytrema melanops* (Raf.). GOLGI method. × 40.

The section is slightly oblique, the left side being farther ventral. It passes through the ventral part of the facial and vagal lobes, illustrating a neurone (*a*) of the intermediate zone of the facial lobe. The dendrites spread throughout the lateral part of the lobe and the neurite passes laterally to enter the substantia reticularis of the oblongata (*s.r.*), here coming into relation with dendrites of the motor VII nucleus, as shown in the figure, and with other motor nuclei. The section shows the position of the dorsal tip of the motor VII nucleus (*n.mot. VII.d.*) and the motor VII root springing from it. The motor VII dendrites which are shown ramifying in the substantia reticularis (*n.mot. VII.v.*) spring from cells of the motor VII nucleus lying ventrally and laterally of those figured and out of the plane of this section. The neurone *b* is drawn in from the section lying next ventrad in the same series.

facial lobe represent the positions of some of the larger of these rosettes. Superficially there is a layer of chief gustatory neurones of the same general form as those of the vagal lobe (Fig. 17), whose neurite springs from the tip of a dendrite and passes at once into the secondary gustatory tract. The peripheral gustatory neurones enter by the communis root of the facial nerve (= dorsal geniculate root of the trigeminus, MAYSER = portio intermedia of WRISBERG in human anatomy) and pass back to the lobe as a huge tract of heavily medullated fibers close to the median line, constituting the pre-vagal portion of the fasciculus communis of OSBORN (= fasciculus solitarius of mammals). Entering the lateral border of the facial lobe, it spreads out in many strands in the superficial layer among the dendrites of the chief gustatory cells (cf. Figs. 5, 16 and 20). These endings are thick, loosely branched arborizations of wide extent. One of the simpler forms of these endings is impregnated in Fig. 18 on the right side.

There is no well defined motor layer of the facial lobe corresponding with that of the vagal lobe, but the ventro-lateral portion along the line of attachment to the oblongata is of different structure from the rest and will be termed the intermediate zone, or *nucleus intermedius facialis*. It contains rather large neurones whose dendrites spread widely through the whole lateral part of the facial lobe and whose neurites reach the substantia reticularis (Figs. 18, *a* and 17, *a* and 8). Here they reach directly the dendrites of the motor VII and less immediately those of the motor V, IX and X nuclei. This is the main pathway for short reflexes from the facial lobe to the oblongata. The absence of a motor layer in the facial lobe which gives rise directly to motor root fibers, like that in the vagal lobe, is to

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a, neurone of the intermediate zone; *asc.s.g.t.*, main ascending secondary gustatory tract; *com.r. VII*, communis (gustatory) root of the facialis; *f.l.m.*, fasciculus longitudinalis medialis; *n.mot. VII.d.*, dorsal part of motor VII nucleus; *n.mot. VII.v.*, ventral part of motor VII nucleus; *mot. VII.r.*, motor root of facial nerve; *r.IX.sen.*, sensory root of the IX nerve; *r.X.mot.*, motor root of the vagus; *r.X.s.*, gustatory root of the vagus; *s.g.t.IX+X*, secondary gustatory tract from X and IX lobes; *s.g. VII.t.*, secondary gustatory tract from the facial lobe; *s.r.*, substantia reticularis; *sp. V*, spinal V tract.

be correlated with the fact that its gustatory impressions come mainly from the outer skin and so give rise to more general body movements, such as turning and seizing, rather than to movements of the intrinsic musculature of the palatal organ, for which the root fibers of the motor layer of the vagal lobe are mainly designed. The substantia reticularis is known to be related not only to the cranial motor nuclei of the branchial or visceral type, as mentioned above, but also to contain cells whose neurites reach the fasciculus longitudinalis medialis and other paths with somatic motor connections (see CAJAL, '96, p. 129 and Fig. 16), so that we have here a very direct mechanism for producing the movement of eye-muscles and trunk-muscles necessary for locating and approaching a sapid substance which has been perceived by contact with taste buds of the outer skin.

2. *Secondary Gustatory Tracts.*

The secondary connections of the vagal, glossopharyngeal and facial lobes are of two general types:—(1) short paths, by way of the intrinsic secondary neurones or of collaterals of the neurites of the chief cells, directly to the motor layer of the vagal lobe and to the substantia reticularis of the oblongata; and (2) long paths to regions above and below the oblongata, arising from the chief gustatory neurones. The connections of the first type are diffuse and largely unmedullated; they have been briefly described above. The connections of the second type are compact well defined tracts of medullated fibers which will be termed the ascending and descending secondary gustatory tracts.

A word of further explanation may be necessary here in justification of the term *gustatory* as applied to these tracts. We have seen above that the communis roots of the VII, IX and X nerves in fishes generally contain fibers from taste buds in the mucous membrane of the mouth or in the outer skin and also fibers which end peripherally by free arborizations unrelated to any specialized sense organs—undifferentiated visceral endings. In view of the fact that these types of fibers, so distinct peri-

pherally, have not as yet been clearly separated at their central terminations, these roots must for the present retain the name "communis system," pending the time when they can be separated into specialized (gustatory) and unspecialized visceral components. With the secondary pathways and centers, however, the first step in this analysis may already be taken, thanks to the advantages of the comparative method.

In forms like the mammals, where the gustatory system is reduced, the analysis of these two elements in the fasciculus solitarius and its associated grey and secondary tracts will probably be impossible save by a degeneration method. The same applies to the amphibia, where the term fasciculus communis was first applied to the homologous structure. In fishes, again, we have some forms with reduced organs of taste, where the problem offers the same difficulties as in the cases cited, and also forms with enormous hypertrophy of the peripheral gustatory system with no appreciable change in the unspecialized component. In the latter cases whatever enlargement of the primary and secondary centers has taken place may clearly be assigned to the gustatory and not to the general visceral system. This is the case presented by the cyprinoid and siluroid fishes particularly, where the whole of the facial lobe and its connections and the greater part of the vagal lobe and connections have clearly arisen in response to the demands of the enormous peripheral gustatory system. While the diffuse connection of these centers with the substantia reticularis is known to have a parallel in the similar connections of the fasciculus solitarius of mammals and therefore doubtless in part pertains to the unspecialized visceral component, the long secondary paths which we here term the secondary gustatory tracts are highly developed only in those fishes possessing elaborate peripheral gustatory systems. This seems to constitute sufficiently good evidence that these long paths are mainly and perhaps wholly gustatory in function.

The neurites of the chief secondary gustatory neurones of the vagal and facial lobes, as we have seen, pass out in thick bundles to the ventro-lateral border of the oblongata, where they

turn to take a longitudinal course parallel with and often almost completely enclosing the spinal V tract. This secondary tract is largely composed of small and feebly medullated fibers, so that in WEIGERT sections it appears paler than the spinal V and the other great longitudinal conduction paths of the oblongata. Part of its fibers turn caudad and part cephalad. We therefore have descending and ascending secondary gustatory tracts (tractus gustus secundus descendens et ascendens) from both the vagal and facial lobes.

(1) Descending Secondary Gustatory Tract.

In the carp, as shown by WEIGERT sections of the adult, the descending tracts from both the vagal and facial lobes are very extensive. From the facial lobe they constitute a massive aggregate of medullated fibers in the "secondary vagus bundle" complex. But the descending tracts from the vagal lobe are largely unmedullated fibers scattered through the substantia reticularis grisea of the oblongata.

The descending secondary facial tract arises, as in Ameiurus, chiefly from the cephalic portion of the lobus facialis. The fibers pass ventro-lateral to gather in a compact bundle mesially and dorsally of the spinal V tract, farther caudad enclosing this tract on all but its external aspect (Fig. 5, *d.s. VII*). There is no obvious addition of descending fibers to this descending bundle in the region of the lobus vagi. It can be easily distinguished from the ascending secondary gustatory tract from the vagal lobe (Fig. 5, *a.s. X*) by the fact that the latter tract is much more feebly medullated at this level.

In the caudal part of the vagal lobe the motor zone is greatly thickened as is also the substantia reticularis grisea, which lies ventro-laterally of it and in intimate relations with the layer of secondary gustatory tracts of the vagal lobe, the descending secondary facial tract and the spinal V tract. This whole area contains descending secondary vagal fibers. These are chiefly very fine unmedullated or feebly medullated fibers passing from the layer of secondary gustatory tracts of the vagal lobe caudad and mesad through the substantia reticularis grisea

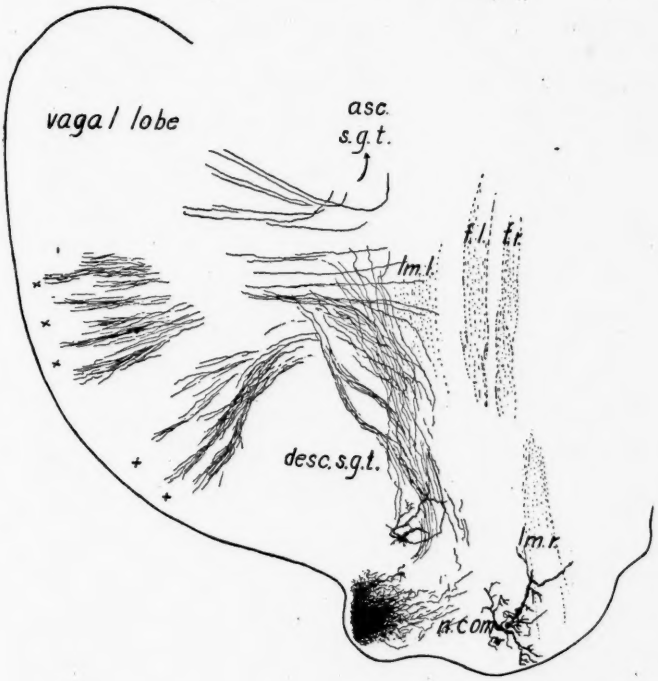

Fig. 19. Longitudinal section through the left vagal lobe of a young carp, 5 cm. long. GOLGI method. × 40.

The section is approximately horizontal, but strongly inclined so that the left side is farther dorsal. It shows the descending secondary gustatory tract (*desc. s.g.t.*) from the vagal lobe to the region of the nucleus funiculi. At the periphery of the vagal lobe in the regions marked by the crosses there is a very rich impregnation of cells among which the secondary fibers arise, which are omitted so as not to confuse the drawing, since they are too densely impregnated to permit an accurate determination of their relations to the fibers. These cells are partly chief secondary neurones like those of Fig. 7, and partly the smaller type as shown in Fig. 11. A very few fibers of the ascending secondary gustatory tract (*asc.s.g.t.*) from the vagal lobe are shown. This tract appears voluminously a few sections ventrad in the position indicated by the arrow. The median line is indicated by the position of the left and right fasciculi longitudinales mediales (*f.l.* and *f.r.*). The lemniscus on both the left (*lm.l.*) and right (*lm.r.*) sides is shown; also the position of the funicular nucleus and commissural nucleus of CAJAL (*n.com.*).

in diffuse formation to reach the region of the nucleus funiculi and commissura infima HALLERI (Figs. 19, 11). The indications are that it springs mainly from the smaller secondary neurones of the lobe (cf. Fig. 11), though I have no conclusive evidence that the chief secondary cells do not also participate in its formation.

In the region of the funicular nuclei the substantia reticularis grisea, related above with the vagal lobe, enlarges. This I term the *inferior secondary gustatory nucleus* (nucleus gustus secundus inferior). It receives the diffuse tracts from the vagal lobe just described, and also the greater part of the descending secondary facialis tract. A portion of the latter tract, however, continues into the spinal cord caudad of the funicular nuclei in the ventro-lateral tracts.

This inferior gustatory nucleus is intimately related with the termini of the spinal V tract, funicular nuclei, commissura infima HALLERI and commissural nucleus of CAJAL. It is clearly a coordination center between gustatory and tactile sensory impressions. In fishes with feebly developed gustatory system it is of insignificant size. Its great development in the cyprinoids and, as we shall see, in the siluroids is correlated with the known feeding habits of these fishes. It has been shown (JUDSON HERRICK, '04) that fishes with taste buds in the outer skin taste with these organs and habitually localize the food stimulus partly by the sense of taste and partly by tactile stimulation of the same cutaneous areas. It may safely be inferred that the descending secondary gustatory connections of these fishes are especially adapted to serve this correlation of the senses of taste and touch as employed in localizing peripheral stimuli in the search for food and to call forth the bodily movements necessary to seize the food when its position has been determined.

The detailed description of these connections involves the discussion also of the secondary connections of the general cutaneous (somatic sensory) system of neurones and must be reserved for a later contribution.

(2) Ascending Secondary Gustatory Tract.

This tract, which takes the greater part of the fibers aris-

ing from the chief secondary gustatory neurones of both the vagal and facial lobes, is one of the most distinctive features of the teleostean brain. In the two groups here treated, particularly, it attains enormous dimensions, constituting the "Sekundäre Vagus-Trigeminusbahn" of MAYSER, whose excellent description ('82, p. 318) is fully confirmed. It is included in the "system γ" of the descriptions of GORONOWITSCH ('88, and '96). The curious notion of B. HALLER ('96, p. 92) that this is a descending tract from the cerebellum and other higher cerebral regions to the sensory centers in the vagal lobe need not detain us, for he gives no evidence for such a view. The common designation of this tract as "secondary vagus bundle" is inadmissible, since in all fishes it contains secondary glossopharyngeus and facialis fibers also, the secondary facialis fibers preponderating in siluroids. Moreover, there are other secondary vagus tracts for general cutaneous and other types of fibers, besides the descending and short gustatory paths described in the preceding section.

The ascending or central gustatory tract takes its position ventrally and mesially of the spinal V and descending secondary facialis tracts and partly enclosing them (Fig. 5, *a.s.X.*). It ascends to the level of the superficial origin of the sensory trigeminus root from the oblongata, where it turns mesially and dorsally to enter its own terminal nucleus (superior secondary gustatory nucleus, Fig. 20). The axial portion of this nucleus was termed by MAYSER "Rindenknoten" and by JOHNSTON ('01) secondary vagus nucleus. It is included in the "Uebergangsganglion" of MAYSER'S descriptions, this latter group of cells being very complex and not as yet fully understood. Its homologies are considered in the final section of this paper.

It lies in the dorsal part of the isthmus ventrally of the line of fusion of the valvula cerebelli with the body of the cerebellum. Typically it lies near the median line and projects into the aquaeductus, but in some cyprinoids it is so greatly enlarged as to reach also to the lateral surface of the brain at the isthmus and there project as a distinct tuberosity between the caudal end of the tectum opticum and the tuberculum acusticum

(Fig. 3, lower figure). It lies cephalad, dorsad and mesad of the motor V nucleus, the long dendrites of some of whose cells pierce it and come into relations with some of the termini of the gustatory fibers (Figs. 21 and 23). The motor V nucleus is very large in these fishes and extends far cephalad and dorsad in intimate relations with the termini of the secondary gustatory tract. The dendrites of these motor cells spread out widely in every direction and are not directed ventro-laterad so generally as in the case of the motor nuclei of the VII, IX and X nerves. In fact, the greater part of them take the opposite course, as figured, into the caudal part of the secondary gustatory nucleus and the adjacent substantia reticularis grisea.

This fact, together with others of similar import, suggests the morphological interpretation of this secondary terminal nucleus; viz., that it is merely a specialization from the substantia reticularis. CAJAL ('96, p. 128) has confirmed the view

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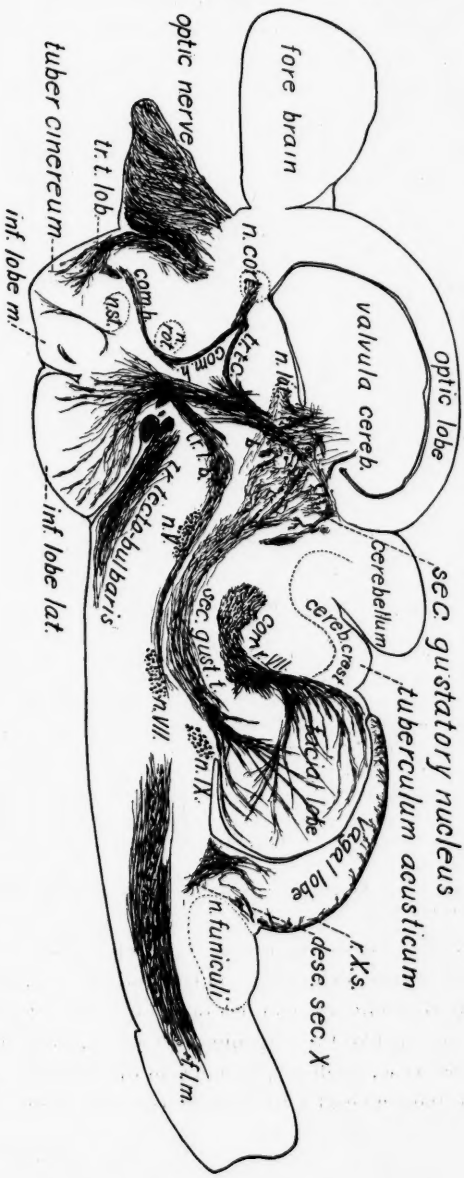
Fig. 20. Parasagittal section through the brain of the spotted sucker, *Minytrema melanops* (Raf.). GOLGI method. × 12.

The sketch is designed to illustrate the course of the ascending secondary gustatory tract and the connections of its terminal nucleus. The plane of the section is slightly oblique so that the caudal end and the ventral side are nearer the median line than are the cephalic and dorsal borders. The figure is a composite, made by outlining one section with the camera lucida and filling in the details from this section and the three sections of the same series on each side immediately adjacent, omitting irrelevant detail. The features introduced are schematized as little as possible. The whole course of the ascending secondary gustatory tract from the facial lobe is shown. The origin of the tract from the vagal lobe lies farther lateral.

b., tract between secondary gustatory nucleus and n. lateralis valvulae; *com.h.*, commissura horizontalis, FRITSCH; *com.r.VII*, communis (gustatory) root of the facialis; *desc.sec.X*, descending secondary gustatory tract from the vagal lobe; *f.l.m.*, fasciculus longitudinalis medialis; *inf.lob.lat.*, lateral lobule of inferior lobe (hypoaria, C. L. HERRICK); *inf.lob.m.*, median lobule of inferior lobe (mammillare, C. L. HERRICK); *n.cort.*, nucleus corticalis, FRITSCH; *n.IX*, motor nucleus of the glossopharyngeus; *n.lat.*, nucleus lateralis valvulae; *n.rot.*, nucleus rotundus, FRITSCH; *n.st.*, nucleus subthalamicus, C. L. HERRICK; *n.V.*, motor nucleus of the trigeminus; *n.VII*, motor nucleus of the facialis; *r.X.s.*, sensory root fibers of the vagus; *sec.gust.t.*, ascending secondary gustatory tract from the facial and vagal lobes; *tr.l.b.*, tractus lobo-bulbaris; *tr.t-c.*, tractus tecto-cerebellaris; *tr.t.lob.*, tractus tecto-lobaris, JOHNSTON (commissura ventralis, C. L. HERRICK). The area marked *n.funiculi* contains also the inferior secondary gustatory nucleus.


fore brain
optic lobe
valvula cereb.
cerebellum
sec. gustatory nucleus
tuberculum acusticum
optic nerve
n. cor.
n. lat.
tr. t. lob.
comm. tect.
comm. tor.
nst.
tuber cinereum
inf. lobe m.
inf. lobe lat.
tr. tect. bulb.
tr. tect. spin.
tr. tect. opt.
n. V.
n. ophthalmicus profundus
n. ophthalmicus superficialis
n. ophthalmicus superficialis
n. maxillaris
n. mandibularis
n. hyomandibularis
n. hyomandibularis
n. palatinus
n. palatinus
n. buccalis
n. buccalis
n. oticus
n. oticus
n. lateralis
n. lateralis
n. lateralis

of KÖLLIKER that the substantia reticularis alba is composed of sensory bundles of the second order and that the substantia reticularis grisea is a sensory field of the third order, designed to distribute sensory excitations from the V, IX and X nerves (and also, it should be added, from the VII nerve) over a large

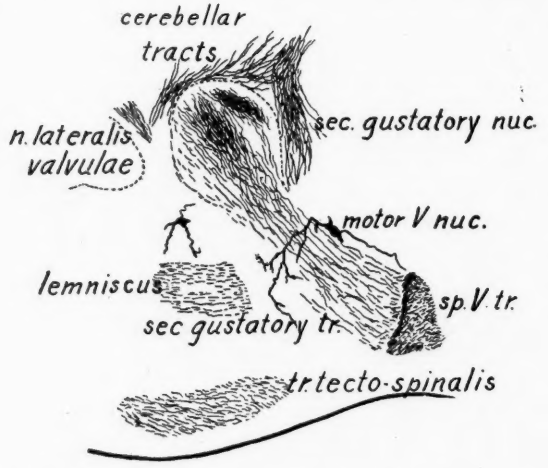


Fig. 21. Portion of a sagittal section of the brain of *Minytrema melanops* (Raf.). GOLGI method. × 40.

The section is quite oblique, the cephalic end and the dorsal side being inclined toward the median line. It passes through the ascending secondary gustatory tract at the point where it enters its terminal nucleus under the cerebellum (the cephalic end of the figure being at the left). The spinal V tract (*sp. V. tr.*) is cut close to its superficial origin from the periphery. A single neurone of the most dorsal part of the motor V nucleus is impregnated, one of its dendrites crossing the mesial side of the gustatory tract to ramify in the most ventral and caudal part of the layer of chief tertiary gustatory neurones, a single one of which is impregnated. The tertiary gustatory path does not lie in the plane of this section (cf. Fig. 23).

field of motor nuclei of the oblongata. This definition, it will be observed, carries also the secondary gustatory nucleus, save that in addition to direct relations of the secondary termini with the motor nuclei, like the trigeminal connection just described, there is here, as we shall see, a much more extensive development of tertiary neurones for connections of a higher order in

the floor of the thalamus (central tertiary tract). The dorsal and mesial position of this derivative of the substantia reticularis is easily explained by the topographic features of the isthmus. Here the ventro-lateral region is occupied by the great conduction paths between the oblongata and the mid-brain—the tractus tecto-spinalis, tractus lobo-spinalis, lemniscus, etc. The dorso-lateral region is occupied by the tuberculum acusticum and its cerebellar connections. The enlarged secondary gustatory terminal is prevented from growing caudad by the great cerebellar crest and tuberculum acusticum. It must, therefore, grow upward, inward and forward into the optocoele. In this position it appears typically in all teleosts. But when still more enlarged, as in cyprinoids, further growth in this direction being prevented by the valvula cerebelli, which is also very large in these fishes, it is forced to grow outward until it appears as a superficial eminence cephalad of the tuberculum acusticum and dorsally of the great ventro-lateral conduction paths just referred to (Fig. 3).

The secondary gustatory nucleus does not, however, comprise the whole of the substantia reticularis grisea of this region of the isthmus. For caudo-mesially of this nucleus at the level where the secondary gustatory tract enters it from the lateral side of the oblongata is another considerable cellular area which represents a less highly specialized portion of the same sensory field. This also borders the ventricle, in some types forming a considerable projection into it from the lateral wall immediately caudad and ventrad of the commissure of the secondary gustatory nuclei. Its anomalous position is brought about by the same forces which were discussed above in connection with the secondary gustatory nucleus. It is in very intimate relation with the motor V nucleus which lies ventro-laterally of it and it apparently is the chief medium of communication between the various sensory pathways and that nucleus. Its neurones, in other words, are like the others of the substantia reticularis grisea in being of the tertiary sensory type and discharging into a motor field, in this case the V nerve. It may therefore be termed the *substantia reticularis grisea trigemini.*

The position of this area of the carp is indicated in Fig. 22. It is reached, as shown in the figure, by a slender branched process of one of the chief tertiary neurones, which may be a dendrite, but more probably is a collateral neurite, though it does not spring from the main neurite (*n*), which enters the tertiary tract separately. The neurone marked *a* lies in the adjacent section and is drawn enlarged in Fig. 25. From the base

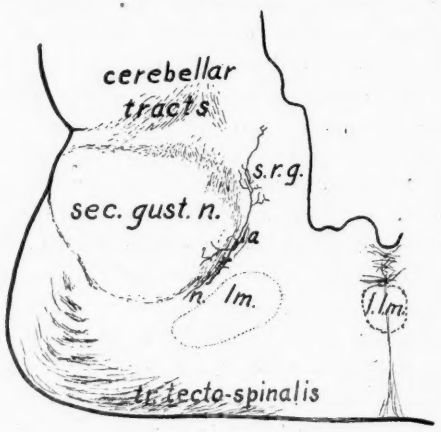


Fig. 22. Section taken through the superior secondary gustatory nucleus of the carp. GOLGI method. ×40.

The section is approximately transverse, but strongly inclined so that the dorsal and right sides are father caudad. A single chief tertiary gustatory neurone is shown, whose neurite (*n*) enters the tertiary gustatory tract. Its main dendrite passes out of the plane of the section (cf. Fig. 25). A much more slender process is completely impregnated, running dorsad and caudad to reach the substantia reticularis grisea trigemini (*s.r.g.*). At *a* is shown the position of the neurone drawn in Fig. 25, which lies in the section adjacent to the one here drawn. The secondary gustatory nucleus is bordered on the dorsal and mesial sides by the fibers of the tertiary tract.

of its neurite is given off a collateral, only a part of which is shown, which is probably of the same type as the one here figured. Contiguous sections of the same series show fibers passing from this area of substantia reticularis directly into the axis of the secondary gustatory nucleus and there arborizing, which probably represent dendrites of the cells of the substantia reticularis which are not impregnated.

These fragmentary data are sufficient to show that we have in addition to direct connections of dendrites of the motor V nucleus with secondary gustatory fibers, a similar but indirect functional connection via the substantia reticularis grisea trigemini. The numerous other connections of the latter area need not now concern us.

One of my GOLGI preparations of the carp shows dendrites of a very large neurone lying in the vicinity of the nucleus of origin of the IV nerve sending dendritic branches ventrad into the region caudad of the commissura ansulata and other large branches farther caudad and laterad into the same portion of the secondary gustatory nucleus which is reached by dendrites of the motor V nucleus. The impregnation is so imperfect that it is impossible to be sure whether this neurone belongs to the motor nuclei of the eye muscle nerves or to the fasciculus longitudinalis medialis or to some other neighboring structure.

3. *Superior Secondary Nucleus and its Connections.*

The superior secondary gustatory nucleus presents, broadly speaking, the same general arrangement as the primary end-station in the vagal and facial lobes. That is, the secondary neurones end in relation with two types of tertiary neurones (1) intrinsic neurones, filling the interior of the nucleus ("Rindenknoten," MAYSER) and (2) the chief tertiary neurones in a dense layer around the periphery. The chief difference between the arrangement of the primary and secondary end-stations lies in the fact that the latter is connected with its fellow of the opposite side by a broad commissure, the commissure of the secondary vagus nuclei of JOHNSTON. As was recognized by MAYSER, this commissure contains fibers of at least two sorts (1) neurites of the intrinsic tertiary neurones, (2) terminals of a portion of the secondary gustatory tract. From (2) it follows that the secondary tracts end partly on the same side and partly in the secondary nucleus of the opposite side, the former portion being much the larger. The uncrossed portion ends by free arborizations within the secondary nucleus and also extensively in the cortical

portion among the chief tertiary cells (Fig. 23). The details of the endings of the crossed fibers I have not been able to observe, but there is every reason to believe that they are essentially similar.

I have no complete impregnations of the intrinsic commissural neurones. The evidence is that their delicate, feebly medullated neurites gather in the interior of the nucleus and terminate after crossing among the dendrites of the chief tertiary neurones of the opposite side. The layer of these chief cells envelopes the secondary nucleus on all sides except where it is interrupted by the secondary and commissural tracts. The neurites of these cells pass directly outward and become medullated as they enter the chief tertiary tract for the inferior lobe. Just external to the layer of tertiary neurones the gustatory nucleus is encapsuled by a dense layer of heavily medullated nerve fibers. These are partly the tertiary fibers, but chiefly cerebellar tracts. The position of the secondary gustatory nucleus in the isthmus is such that the cerebellar penduncles, passing downward from the cerebellum and valvula, almost entirely envelop it. It is this peculiarity which suggested to MAYSER the name "Rindenknoten." Surrounding this fibrous capsule is an aggregate of nuclei with very diverse connections to which MAYSER applied STIEDA'S name, "Uebergangsganglion."

This region is perhaps the most intricate and difficult of analysis in the teleostean brain, as it contains several large centers and numerous important tracts, both medullated and unmedullated, all crowded into a very small space. The dorsal part of the isthmus is more than usually crowded in these types, not only by these great gustatory centers, but also by the enlarged cerebellum and valvula and their associated tracts.

The broad line of fusion of the valvula cerebelli with the torus semicircularis (colliculus) is occupied by a very dense mass of cells and medullated and unmedullated tracts whose relations are only imperfectly shown in my preparations. The whole complex, which lies mesially of the nucleus lateralis mesencephali (EDINGER), or colliculus, I term provisionally the nucleus lateralis valvulae. It is, apparently, the most cephalic

part of the "Uebergangsganglion" of STIEDA. This group of cells fuses behind with the dorsal and cephalic border of the secondary gustatory nucleus, but is separated from it more or less definitely by the medullated vertical cerebellar tracts which encapsule the secondary gustatory nucleus. Sections stained by the method of PAL show large tracts of fine fibers with ex-

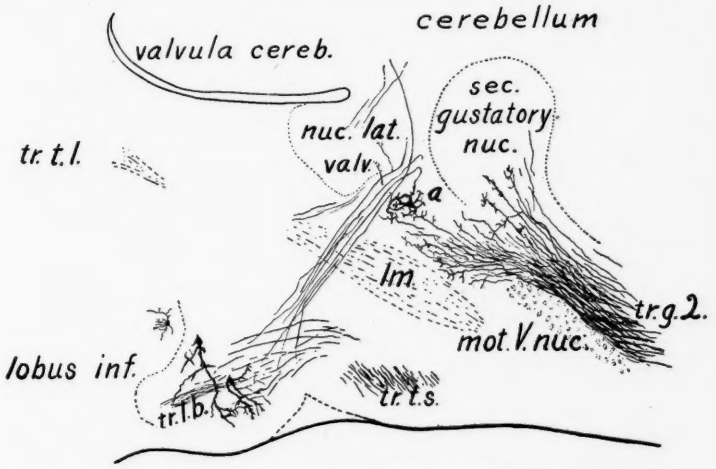


Fig. 23. Portion of sagittal section of the brain of a young carp, 5 cm. long. GOLGI method. × 40.

The ventral side of the preparation is below and the cephalic end at the left. The section includes the superior secondary gustatory nucleus ("Rindenknoten," MAYSER) and shows the origin and course of the tertiary path to the inferior lobe. A single neurone of the latter type is impregnated completely (*a*) save for the terminal arborization. Mingled with the neurites of these cells are those of the tract between the cerebellum and the inferior lobe (tractus lobo-cerebellaris, EDINGER). Among the terminals of the tertiary tract are the cells of origin of the tractus lobo-bulbaris et spinalis (*tr.l.b.*); *l.m.*, lemniscus; *tr.t.l.*, tractus tecto-lobaris; *tr.t.s.*, tractus tecto-spinalis.

ceedingly delicate medullary sheaths passing dorso-ventrally between the n. lateralis valvulae and the cerebellum and valvula (Fig. 24), and GOLGI sections show diffuse unmedullated tracts taking the same courses (Fig. 20). Whether the medullated and the unmedullated fibers spring from neurones of the same type, I have not been able to determine. The neurones shown

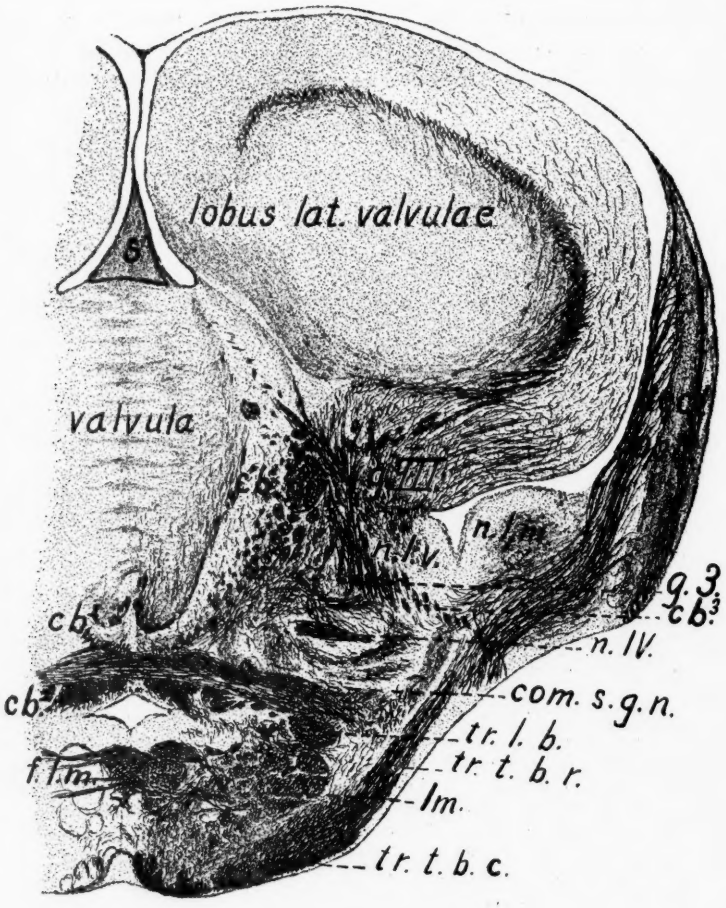


Fig. 24. Transection through the brain of a large carp just cephalad of the superior secondary gustatory nucleus. Stained by the method of WEIGERT-PAL. × 20.

The section passes through the most cephalic portion of the commissure of the secondary gustatory nuclei, and illustrates the relations of the nucleus lateralis valvulae to this nucleus and to the cerebellum. The trochlearis (*n. IV.*) decussates just cephalad of the gustatory commissure and in passing to its super-

by the GOLGI sections are like the cells of the granular layer of the cerebellum and probably are of that type, receiving afferent cerebellar impulses and transmitting them to the cortex cerebelli. Whether they receive their impulses from the adjacent gustatory nucleus or from other sources, my preparations do not show with certainty, but probably partly from the former.

There is also a broad unmedullated connection between the ventral part of the secondary gustatory nucleus and the cephalic part of the n. lateralis valvulae, running cephalad through the vertical cerebellar tracts (designated by *b* in Fig. 20). Horizontal sections of the brain of Catastomus show numerous delicately medullated fibers running between the whole cephalic face of the gustatory nucleus and the n. lateralis valvulae. These connections lend further support to the belief that the n. lateralis valvulae is in part a gustatory intermediary station for the cerebellum. This nucleus extends cephalad to the point where the valvula severs connection with the floor of the mesencephalon and here a large tract passes between its cephalic end and the nuclei of the third nerve and of the fasciculus longitudinalis which lie mesially of it. It is no doubt this connection which led B. HALLER to state ('98, p. 522) that the "Uebergangsganglion of FRITSCH and MAYSER is an "upper motor oculomotorius nucleus." The nucleus lateralis valvulae

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ficial origin become embedded in the most cephalic part of the secondary gustatory nucleus, the latter being represented in the figure by the neuropil surrounding *n.IV.* Sections immediately caudad show the gustatory nucleus occupying the entire space from near the median line to the lateral surface of the brain and from the level of the commissural fibers and tr. lobo-bulbaris (*tr.l.b.*) up to the valvula cerebelli.

cb., cb^1., cb^2., cb^3., cerebellar tracts; *com.s.g.n.*, commissure of the secondary gustatory nuclei; *f.l.m.*, fasciculus longitudinalis medialis; *g.III*, fibers arising from the granule cells of the nucleus lateralis valvulae and passing dorsally into the lateral lobe of the valvula cerebelli; *g.3.*, tertiary gustatory tract for the inferior lobe appearing as oval bundles among the strands of the cerebellar tract cb^3.; *lm.*, lemniscus (fasciculus lateralis); *n.IV.*, root of the fourth nerve; *n.l.m.*, the extreme caudal end of the nucleus lateralis mesencephali (torus semicircularis, colliculus); *n.l.v.*, nucleus lateralis valvulae; *s.*, a large blood sinus between the lateral lobes of the valvula; *tect.opt.*, tectum opticum; *tr.l.b.*, tractus lobo-bulbaris; *tr.t.b.c.*, tractus tecto-bulbaris et spinalis cruciatus; *tr.t.b.r.*, tractus tecto-bulbaris et spinalis rectus.

has other connections (with the substantia reticularis of the oblongata, optic thalamus, etc.) which I have not yet fully worked out. Its homologies are discussed briefly beyond. Another part of the "Uebergangsganglion" which serves as a gustatory reflex center is the nucleus already designated as substantia reticularis grisea trigemini. There remain several considerable collections of cells in the "Uebergangsganglion" which may have gustatory functions, but their discussion would involve a more extensive analysis of the mesencephalon than we can here attempt.

A typical illustration of the chief tertiary gustatory neurones in the cortex of the secondary gustatory center of the carp is seen in Fig. 25. The dendrite plunges into the axial portion of the nucleus ("Rindenknoton," MAYSER) and there spreads out widely among the termini of the secondary gustatory fibers (cf. Figs 22, 23). The neurite passes downward to enter at once the tertiary gustatory tract for the inferior lobe of the same side, where it takes up a dense medullary sheath and so is rarely completely impregnated in GOLGI preparations. These medullated fibers mingle immediately with similar ones of the cerebellar tracts (lobo-cerebellaris and others) which encapsule the secondary nucleus and which likewise pass into the inferior lobe, so that I have found it impossible in WEIGERT sections to effect the separation of the two classes of fibers except at the origin of the tertiary gustatory tract from its nucleus. I have, fortunately, secured a sufficient number of complete GOLGI impregnations to show the origin of the tract without uncertainty. Its entire extent save the terminal arborization is shown in Fig. 23.

The combined tract passes ventrad and somewhat cephalad to enter the caudal border of the inferior lobe and spread throughout the whole of the lateral lobule of this organ. Whether any of these fibers reach the median lobule my preparations do not definitely determine, but apparently not. (The terms lateral and median lobules are used in the sense defined by DAVID ('92). The lateral lobules are the hypoaria and the median lobules the mammillary bodies of C. L. HERRICK ('92)).

The terminal arborizations of this tract in the inferior lobe of Ameiurus shown in Fig. 37 probably belong to the gustatory component.

The *tractus lobo-bulbaris* arises from the whole of the lateral lobule of the inferior lobe and its fibers mingle with those of the tertiary gustatory tract, the two tracts, however, being well separated where they leave the lobe (Fig. 20, 23). The tractus lobo-bulbaris is the main path for descending impulses from the inferior lobe (gustatory and other reflexes) and was termed in MAYSER'S descriptions ('82, p. 319) "Nervenfaserbahn *x*."

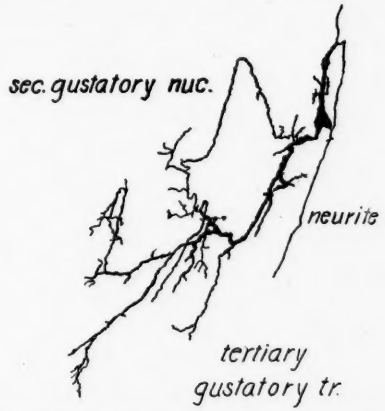


Fig. 25. One of the chief tertiary neurones of the superior secondary gustatory nucleus of a young carp. GOLGI method. × 187.

For the relations of this neurone to the surrounding structures, cf. Fig. 22, which is drawn from the section next caudad. The dendrites spread out in the mesial part of the secondary gustatory nucleus. The neurite at once enters the tertiary gustatory tract for the inferior lobe and either passes out of the plane of the section or becomes medullated and so fails to impregnate.

The fact that it is larger (as mentioned by MAYSER) in cyprinoids and the peculiarities of its course in the oblongata make it probable that it is the chief motor return path for the higher gustatory reflexes. This of course is not its only function, for it clearly serves as the chief path for all descending impulses from the inferior lobe to the oblongata and cord, and therefore carries olfactory and other reflex impulses in addition to gustatory.

The course of the tractus lobo-bulbaris as it leaves the inferior lobe is clearly shown in some of my GOLGI preparations. In WEIGERT sections this tract is so confused at its origin with the fibers of the tractus lobo-cerebellaris and tertiary gustatory path that it cannot be clearly distinguished at first. Its fibers throughout their course are very fine and feebly medullated. The tract passes up from the inferior lobe and arches around the ansulate commissure to turn caudad along the inner border of the lemniscus. Upon reaching the level of the secondary gustatory nucleus it turns laterad over the dorsal surface of the lemniscus (Fig. 24) and takes up a position ventrally of the secondary gustatory nucleus (Fig. 20, *tr.l.b.*). Farther back it becomes partially enveloped by the ascending fibers of the secondary gustatory tract. The latter tract in cross section is crescent-shaped and the concavity of the crescent, which faces inward, is occupied by the descending fibers of the tractus lobo-bulbaris. This tract is thus placed along the dorso-lateral border of the substantia reticularis, which, as we have seen, is the chief avenue of communication with the motor nuclei of the oblongata. The tractus lobo-bulbaris diminishes caudad, breaking up in the substantia reticularis and so puts the gustatory center in the inferior lobe into relation with the peripheral musculature. It doubtless extends into the spinal cord, but it is impossible to distinguish its fibers from the others in the substantia reticularis alba farther back than the vagal lobes.

SECTION IV. THE CENTRAL GUSTATORY SYSTEM OF SILUROID FISHES.

As we have seen above, the anatomy and physiology of the peripheral gustatory system of the cat fishes, or horned pouts, is now well known. The cutaneous portion of the system is here hypertrophied, while the buccal portion is about as in other fishes. This is the explanation of the fact that the cat fishes possess enlarged facial lobes, while the vagal lobes are of the typical teleostean form. We shall now proceed to a description of the internal anatomy and secondary connections of these structures in Ameiurus and closely related species. The mater-

ial consists of serial sections of ten adult brains cut in the three conventional planes and stained with DELAFIELD'S hæmatoxylin and by the methods of WEIGERT and WEIGERT-PAL, together with serial sections of about 100 younger brains prepared by the method of GOLGI and cut in various planes.

The *vagal lobe* of the cat fish is essentially similar to that of most other teleosts. The general relations as seen in transections stained by DELAFIELD'S hæmatoxylin are shown in Fig. 26. The lobe is crowded with numerous small nerve cells,

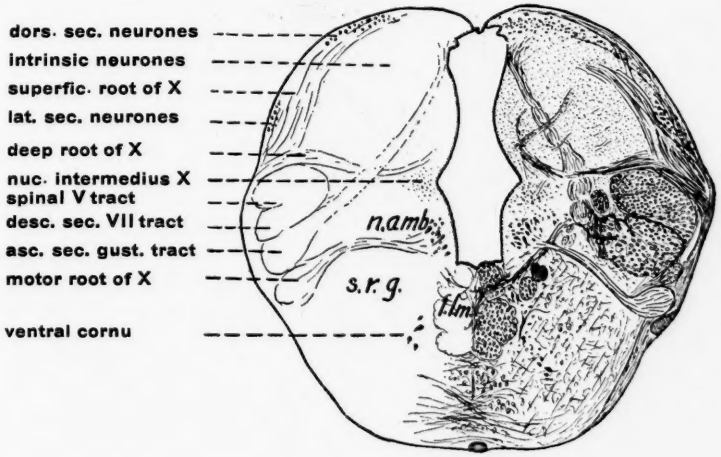


Fig. 26. Transverse section through the vagal lobes of a large adult of *Ictalurus punctatus* (Raf.). Drawn from a hæmatoxylin preparation. ×16.

f.l.m., fasciculus longitudinalis medialis; *n.amb.*, nucleus ambiguus; *s.r.g.*, substantia reticularis grisea.

which take up a very pale stain in hæmatoxylin. Most of these intrinsic cells are neurones of GOLGI'S type II, whose processes do not extend beyond the lobe. Along the dorsal and lateral borders of the lobe is a layer containing larger cells whose nuclei stain very little in hæmatoxylin and whose cytoplasm practically not at all. The axones of these cells constitute the chief sensory conduction paths from the vagal lobe to other parts of the brain, and I shall term them the dorsal

and lateral chief secondary gustatory neurones. Deeply embedded in the substance of the medulla oblongata ventrally of the main body of the vagal lobe is an area filled with cells somewhat larger than the intrinsic neurones but much smaller than the chief secondary neurones, which may be termed intermedi-

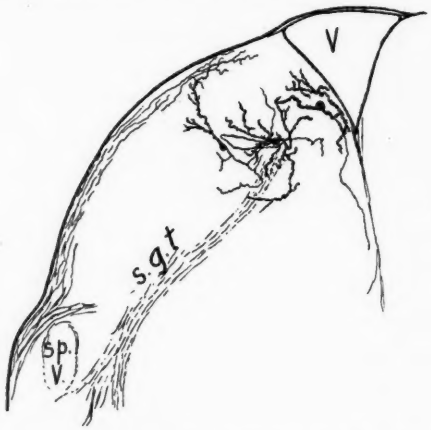


Fig. 27. Three intrinsic neurones of type II from the left vagal lobe of *Ameiurus nebulosus*. From a GOLGI preparation. × 60.

The secondary communis tract (*s.g.t.*) which appears to arise among these cells, in reality springs from cells lying farther dorsally which are not impregnated in this preparation. Superficial root fibers of the vagus are impregnated at the border of the vagal lobe. *sp. V.*, spinal V tract; *V*, ventricle.

ary neurones (nucleus intermedius vagi). Their neurites enter the substantia reticularis and other conduction pathways between the sensory and motor nuclei. Ventrally of the vagal lobe and not properly to be considered a part of it is the nucleus ambiguus, close to the median line in the floor of the fourth ventricle. The communis roots of the IX and X nerves enter the lobe at its ventro-lateral border, some descending along the lateral aspect of the oblongata to the region of the commissura infima HALLERI, forming the descending communis root of the vagus, others passing directly inward under the lobe to terminate in the lobe along its inner or ventricular border, forming the deep communis roots of the vagus and glossopharyngeus, while

the main portion of the root fibers turn dorsally along the outer aspect of the vagal lobe to form the superficial communis roots of these nerves.

Communis root fibers, presumably bearing both general visceral and gustatory impulses, arborize freely in the entire inner, dorsal and lateral surfaces of the vagal lobe, some arbor-

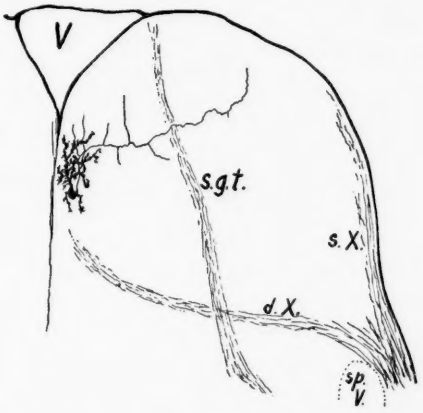


Fig. 28. An intrinsic neurone of the right vagal lobe of *Ameiurus nebulosus* seen in cross section. The cell body lies near the mesial border of the right vagal lobe and the neurite is directed laterally through the middle of the lobe. From a GOLGI preparation. ×60.

d.X., deep root of the vagus; *s.g.t.*, secondary gustatory tract; *sp.V.*, spinal V tract; *s.X.*, superficial sensory root of the vagus; *V*, ventricle.

izations also occurring in the center of the lobe. Impulses from the latter are taken up by the intrinsic cells and diffused throughout the entire lobe. For the forms of these cells see Figs. 27, 28, 29, 30, 34. It may be conjectured that these cells receive mainly the unspecialized visceral root fibers, since the gustatory fibers are here, as in cyprinoids, almost certainly related chiefly to the superficial groups of secondary neurones. Type II cells are abundant in elasmobranchs (HOUSER, '01), whose taste buds are few and confined to the mouth, but were not demonstratable in any of JOHNSTON'S GOLGI preparations of

Petromyzon ('02), though the secondary neurones of type I were found about as in teleosts. It Petromyzon, it is interesting to note in this connection, the cutaneous terminal bud system is well developed.

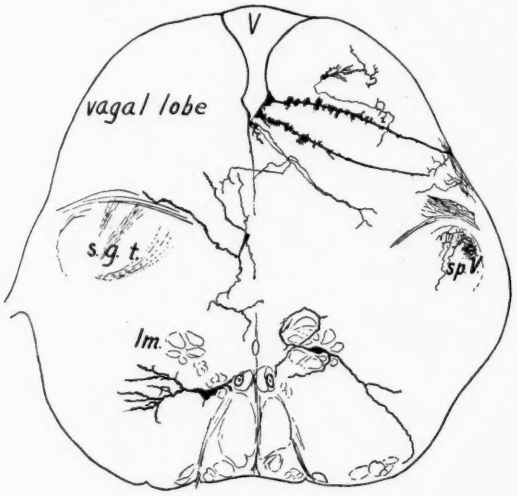


Fig. 29. Transverse section through the vagal lobes of *Ameiurus nebulosus* illustrating a type II cell within the vagal lobe similar to those in Figs. 27 and 28; also two other small cells at the ventral angle of the fourth ventricle, whose neurites terminates among the intermediary neurones of the same and opposite side. One of the latter cells is impregnated; also a ventral horn cell on the left side. Two supporting fibers of the neuroglia system are shown on the right side. GOLGI method. × 50.

l.m., lemniscus; *s.g.t.*, secondary gustatory tracts; *sp.V.*, spinal V tract; *V.*, ventricle.

The root fibers which end on the surface of the vagal lobe spread out in very wide arborizations (Figs. 30 and 31). These are most densely massed in two regions in intimate relation with the two groups of chief secondary neurones already referred to as the dorsal and lateral secondary gustatory neurones (Fig. 26). The general relations of the two groups of superficial secondary neurones are indicated in Fig. 31, where a dense neuropil richly

impregnated indicates the positions of these two chief centers of secondary connection for gustatory root fibers.

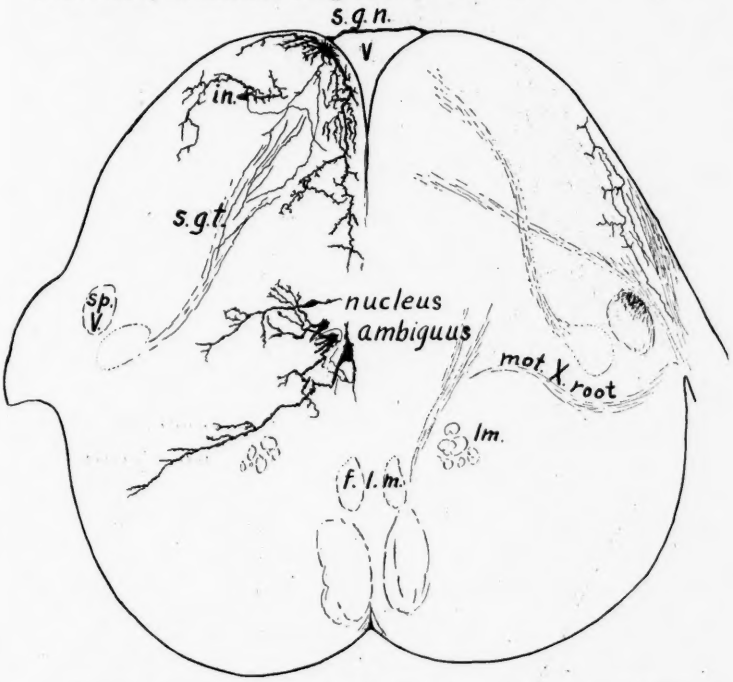


Fig. 30. Transverse section through the vagal lobes of *Ameiurus nebulosus*. GOLGI method. ×60.

On the left side is shown a gustatory neurone of the dorsal secondary group (*s.g.n.*), whose neurite enters the secondary gustatory tract (*s.g.t.*). The preparation shows one of the intrinsic neurones of the vagal lobe (*in.*), also several cells of the nucleus ambiguus. On the right side are seen some of the simpler terminations of the communis root of the vagus.

The dorsal portion of the superficial roots of the vagus and glossopharyngeus is the most important member of the complex. Its fibers arborize intimately intertwined with the thick thorny dendrites of the dorsal secondary neurones (Figs. 30, 31, 32). These are very highly differentiated cells whose neurites arise from the cell body and constitute the secondary gustatory tract, or central gustatory path. Their dendrites are

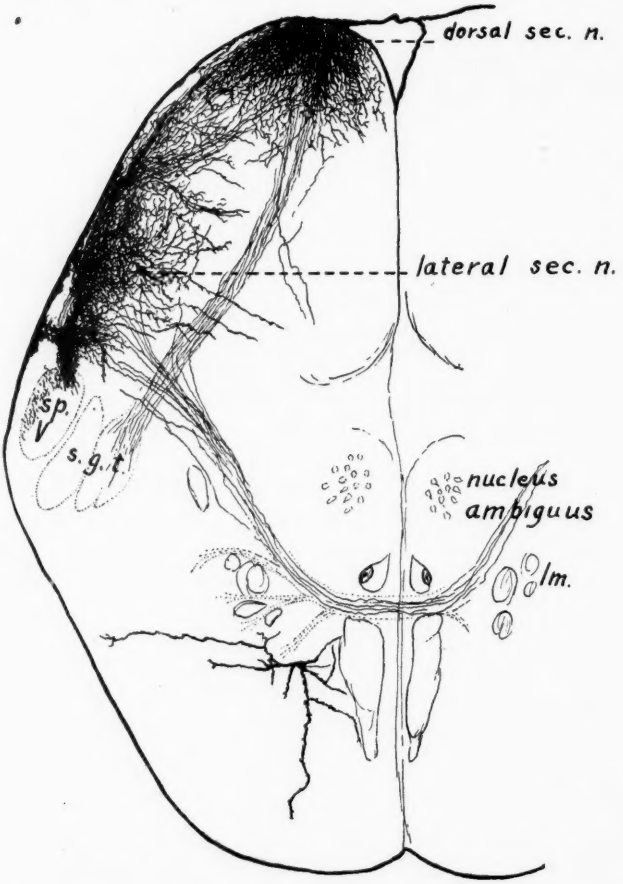


Fig. 31. Transverse section through the cephalic part of the vagal lobes of *Ameiurus nebulosus*. From a GOLGI preparation. × 90.

It illustrates the general relations of the termini of the gustatory fibers of the vagus. Dorsally these root fibers form dense arborizations about cells of the dorsal secondary group of the vagal lobe (*dorsal sec.n.*), and ventrally about cells of the lateral secondary group (*lateral sec.n.*). From the dorsal group neurites pass downward and outward into the secondary gustatory tract (*s.g.t.*); from the lateral group neurites pass to the opposite side through the ventral commissure (cf. Fig. 33).

very thick, thorny and much branched, interlacing with the root fibers to form a very dense neuropil in the most superficial layer of the vagal lobe.

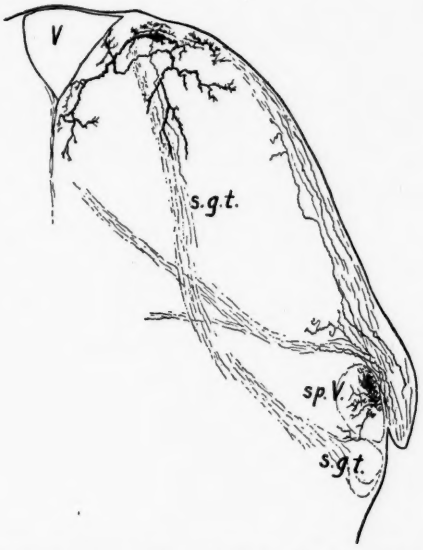


Fig. 32. Transverse section through the vagal lobe of *Ameiurus nebulosus*, illustrating a secondary gustatory neurone similar to that shown in Fig. 30. GOLGI method. × 60.

As the figures show, they are very unlike the corresponding cells of the vagal lobe of the larger cyprinoid fishes, whose minute cell bodies are closely crowded around the periphery with the bushy dendrites thrust directly inward and giving off at the apex the neurite. These cells are exceedingly numerous in the carp and relatively few in the cat fish, and this fact doubtless explains the difference in form. Probably neither type is very near the primitive form. JOHNSTON figures in his Petromyzon paper ('02, Figs. 7 and 21) chief cells of the vagal lobe of Lampetra whose cell bodies lie close to the ventricle and give off the neurite directly, while the busy dendrite is directed toward the periphery. HOUSER ('01) unfortunately secured no impregnations of the chief gustatory cells of the shark, his prep-

arations showing only the intrinsic type II cells. In Acipenser JOHNSTON ('01) finds these cells similar to my impregnations of the cyprinoids, but much simpler.

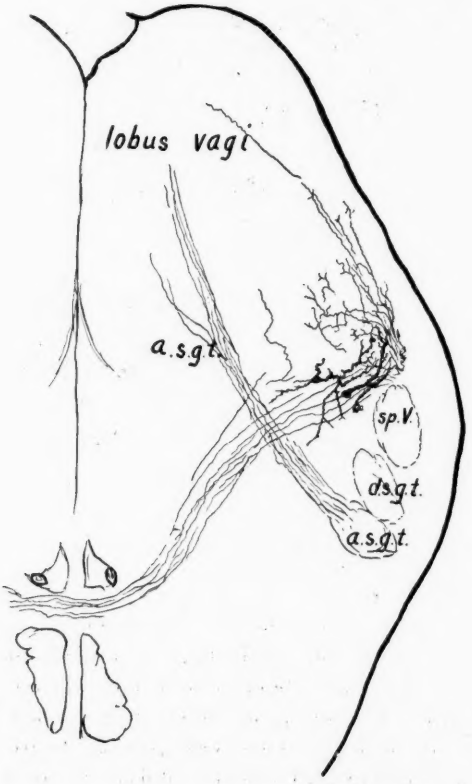


Fig. 33. Portion of a transverse section through the oblongata of *Ameiurus nebulosus* in the cephalic part of the vagal lobe. From a GOLGI preparation. × 90.

The section illustrates terminal arborizations of the most cephalic fibers of the gustatory root of the vagus among the dendrites of the neurones of the lateral secondary group and the course of the neurites from the latter through the raphé toward the substantia reticularis of the opposite side. *a.s.g.t.*, ascending secondary gustatory tract from vagal lobe; *d.s.g.t.*, descending secondary gustatory tract from facial lobe; *sp. V.*, spinal V tract.

The neurites from the cells of the lateral secondary gustatory nucleus are in the main directed across the raphé through the ventral commissure to reach the substantia reticularis grisea of the opposite side of the oblongata (Figs. 31, 33). Here they may come into relation with the dendrites of the nucleus ambiguus and other motor nuclei. They are to be regarded as direct reflex paths, differing from those provided by the intermediary neurones in that there is no type II cell interpolated between the root fiber and the tract neurone. Since this arrangement prevails also for the main ascending gustatory path, it is probable that this is the path of direct motor reflexes excited by the gustatory communis root fibers rather than by the unspecialized visceral element.

The dorsal and lateral groups of chief secondary neurones receive by far the greater part of the vagal communis root fibers, and since most of these root fibers are gustatory in function, we may infer with great confidence that the more lateral group of secondary neurones is the chief path for direct gustatory reflexes in the medulla oblongata and spinal cord, while the more dorsal group is the main ascending or central gustatory path.

Neurites from the dorsal group of secondary neurones pass through the middle of the vagal lobe in slender compact bundles, directed downward and outward to a position ventrally of the spinal V tract. Here they turn and take a longitudinal direction, most turning cephalad and constituting the ascending secondary gustatory tract ("sekundäre Vagusbahn," MAYSER), but some caudad. The latter are derived chiefly from the more lateral part of the vagal lobe and more probably should be relegated to the cells of the more lateral group of neurones. The relations of the ascending fibers from the vagal lobe and both the ascending and the descending fibers from the facial lobe are indicated in Fig. 37.

The relations of the cells of the intermediary nucleus of the vagal lobe are not very clearly brought out in my preparations. Figs. 29 and 34 show their dendrites in relation with the neurites of type II cells of the vagal lobe. Some prepara-

tions suggest that the neurites of these cells end in relation with cells of the nucleus ambiguus. Other preparations show their neurites extending out into the substantia reticularis (right side of Fig. 34), and still others show their neurites passing into the decussating tract for the ventral commissure, probably for the

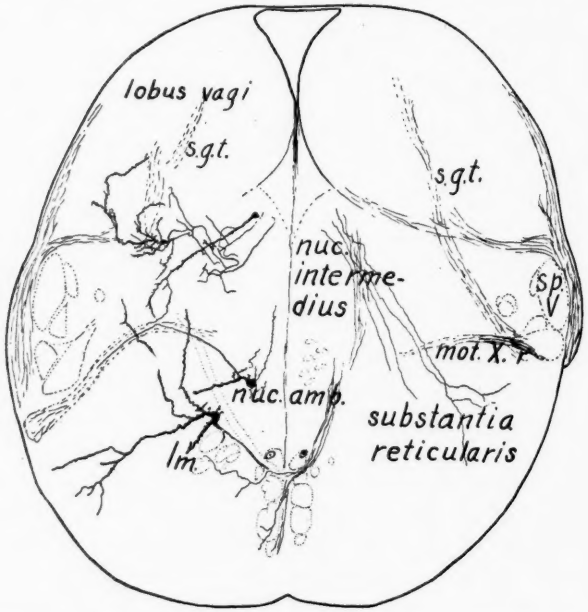


Fig. 34. Transection through the vagal lobes of *Ameiurus melas*. GOLGI method. × 50.

The figure shows on the left an intrinsic neurone whose neurite (of type II) arborizes in the nucleus intermedius. One neurone of the latter nucleus is impregnated, though only the proximal part of the neurite is shown. On the opposite side similar neurites are seen to enter the substantia reticularis grisea and the tract for the ventral commissure.

substantia reticularis of the opposite side. Completely impregnated neurones of the latter type are figured by VAN GEHUCHTEN ('94, Plate I, Fig. 13) for the trout. Some of these neurites reach the level of the commissura infima Halleri and arborize among the cells of the commissural nucleus of CAJAL. In

this way are provided extensive pathways for vagus reflexes both of the gustatory and unspecialized visceral type. This layer of intermediary neurones extends caudad from the vagal lobes directly into the commissural nucleus and the latter is probably in part a differentiation from it. The motor layer of the vagal lobe of cyprinoids occupies the position corresponding to these intermediary neurones, but the structures are not exactly equivalent. These cells are probably represented in the carp by intrinsic neurones which send their neurites into the substantia reticularis. I have no preparations of Ameiurus showing motor root fibers springing from this nucleus, such as arise from the motor layer of the vagal lobe of the carp. Here, as in the cyprinoids, there is no direct path between the termini of the primary gustatory root fibers and the motor nuclei of the oblongata. The most direct return reflex path is by way of the nucleus ambiguus whose neurites pass directly out to the striated branchial musculature. But the dendrites of these cells in no case come into relation with the termini of sensory root fibers. On the other hand, they ramify in the substantia reticularis (Fig. 30) and at least one neurone is always intercallated between them and the sensory root fibers. A similar relation prevails for the connections with the other motor nuclei.

The *facial lobes* of Ameiurus are considerably larger than the vagal lobes and each is incompletely divided into mesial and lateral lobules by a shallow fissure. Both lobules receive the terminals of the very large communis root of the facial nerve, this root entering the lobus from in front at its ventrolateral border and spreading out in many strands which pass upward through the lobe to reach its exposed surfaces. The internal structure is in general similar to that of the vagal lobes. There are numerous very small intrinsic neurones and larger secondary neurones bordering the surface, which differ somewhat in form from those of the vagal lobe.

Fig. 35 shows some of the simpler types of endings of the root fibers. The interior of the lobe in occupied by intrinsic neurones of type II which are similar to those of the vagal lobe (Fig. 35 *in.*). The secondary connections are likewise essen-

tially similar. The large tract of descending neurites shown in Fig. 37 passing from the facial lobe arises from the lateral part of the lobe, while the ascending secondary tract, or central gustotory path, takes its origin from the more mesial portion of the dorsal surface. These chief gustatory neurones of the facial lobe are like those of the vagal lobe in staining reaction, position and general relations. They are, however, smaller with more slender dendrites. One of them is shown in the dorsal

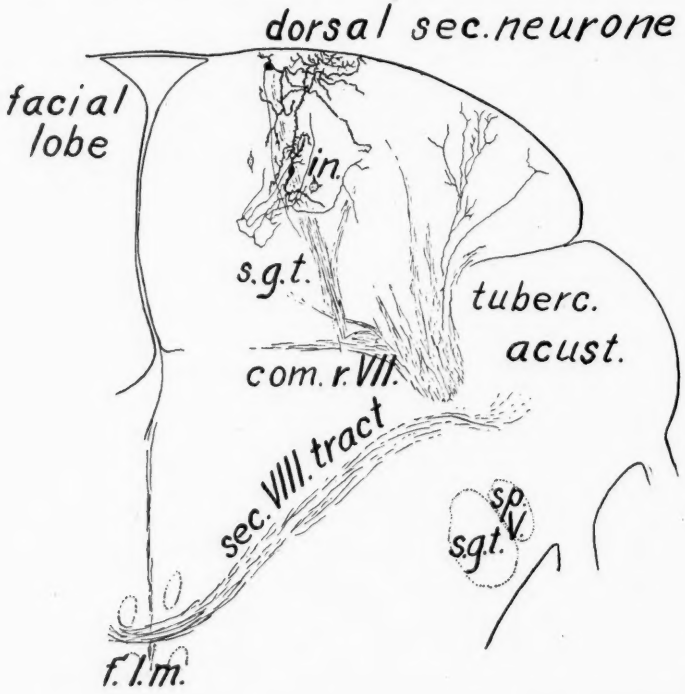


Fig. 35. Portion of a transection though the cephalic end of the right facial lobe of *Ameiurus nebulosus*. GOLGI method. × 60.

The communis (gustatory) root of the facialis (*com.r. VII.*) enters from below. Dorsally is a single impregnated chief secondary neurone whose neurite enters the secondary gustatory tract (*s.g.t.*), and below it is an intrinsic neurone of type II (*in.*).

part of Fig. 35 and another as seen from above in horizontal section in Fig. 36. Ventro-mesially of the facial lobe, especially its caudal part, is a region of sparse cells which extends caudad to join the intermediate nucleus of the vagal lobe. It will be termed the intermediate nucleus of the facial lobe and is strictly comparable with the corresponding region of cyprinoids.

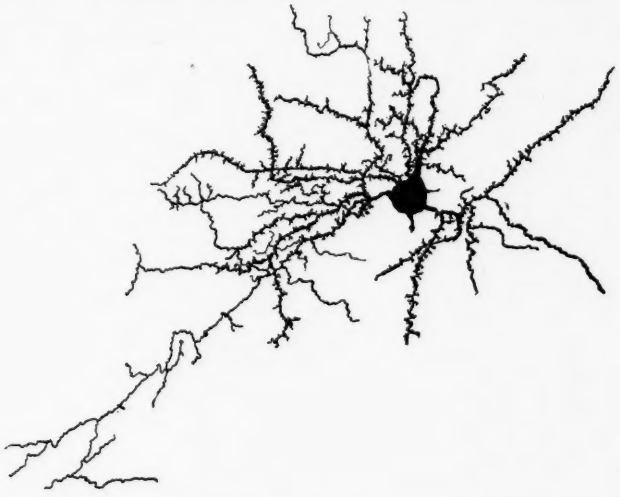


Fig. 36. A secondary neurone of the dorsal part of the facial lobe of Ameiurus as seen from above. GOLGI method. × 500.

Drawn from a horizontal longitudinal section passing through the extreme dorsal part of the facial lobe. The neurite extends ventrally at right angles to the plane of the section (cf. Fig. 35) and hence of course does not appear in this preparation.

The greater part of the chief gustatory neurones of the vagal and facial lobes, as we have seen, send their neurites into the ascending secondary gustatory tract, or central gustatory path (secondary vagus bundle of MAYSER). This ascending tract terminates in the secondary gustatory nuclei under the cerebellum, partly on the same side and in smaller numbers on the opposite side. These nuclei lie in the isthmus close under the cerebellum at the point where the body of this organ is joined by the valvula cerebelli. The two nuclei are connected

by a broad dorsal commissure, above which is a commissure of the acustico-lateralis centers lying under the lateral extensions of the cerebellum. They are enveloped on all sides by tracts of fibers running vertically between the cerebellum and the regions in the brain stem below and cephalad of the nuclei, the cerebellar tracts forming a sort of capsule around the grey nuclei, these relations being the same as already described for cyprinoids. The relations of this nucleus and its tracts are shown in Fig. 37.

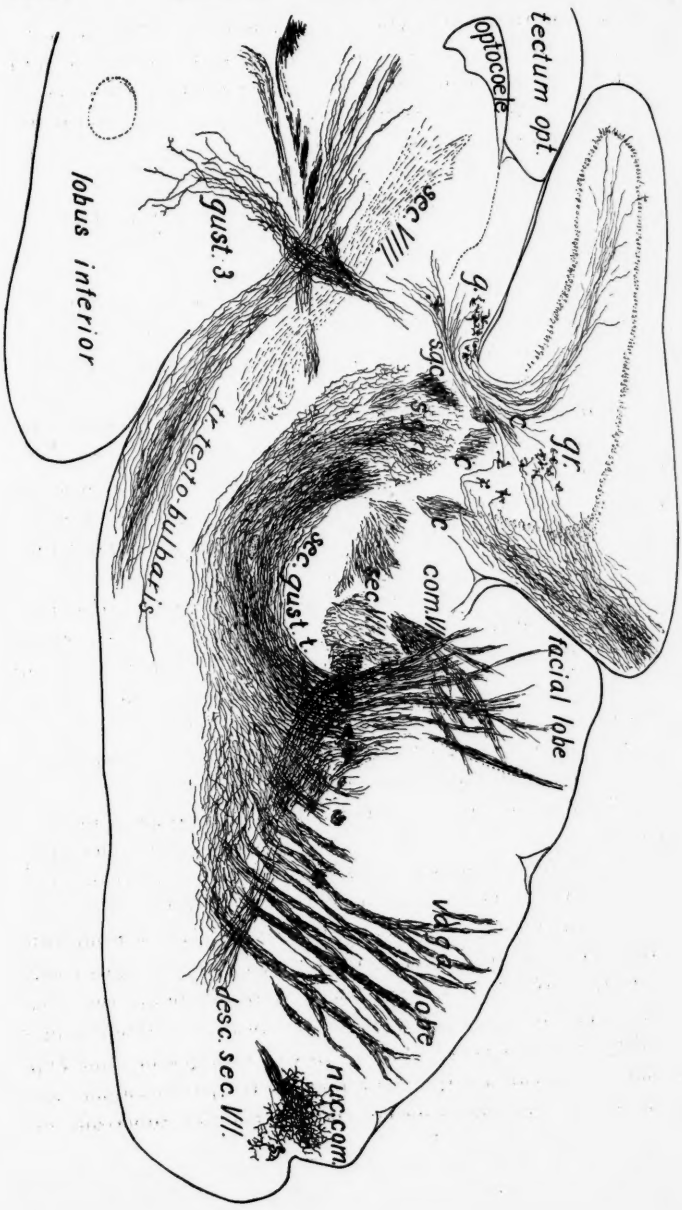
The intrinsic neurones of these nuclei are rarely well impregnated in my GOLGI preparations. The fibers of the central gustatory path end for the most part in free arborizations among these cells without crossing. But some of the tract fibers are clearly seen to cross to the opposite nucleus through the commissure of the secondary gustatory nuclei, as MAYSER has stated.

The tertiary tract arises from the chief cells in the cortical portions of the nucleus. These are frequently impregnated

Fig. 37. A parasagittal section taken through the brain of *Ameiurus nebulosus* so cut as to pass through about the middle of one vagal and one facial lobe and the lateral part of the cerebellum (cf. Figs. 5 and 20). Drawn from a single GOLGI preparation. × 45.

The section shows nearly the whole course of the central gustatory path (*sec.gust.t.*), composed of neurites of the chief secondary gustatory neurones of the vagal and facial lobes which terminate in the secondary gustatory nucleus (*s.g.n.*) under the cerebellum. The origin of the facial portion of the descending secondary gustatory tract (*desc.sec. VII.*) is seen in the facial lobe. In the facial lobe there is also seen a portion of the lateral part of the communis root of the facial nerve (*com. VII*) passing up to arborize within the lobe. The neurones of the vagal and facial lobes, which were richly impregnated in the preparation, are omitted from the drawing for the sake of simplicity. Along the cephalic border of the secondary gustatory nucleus is the beginning of the secondary gustatory commissure (*s.g.c.*). The origin of the tertiary gustatory tract from the secondary nucleus is not shown, but the terminations of these fibers (*gust.3*) are illustrated in the inferior lobe.

Bundles of fibers from the tuberculum acusticum are seen under the facial lobe, where they decussate, and their termini in the nucleus lateralis mesencephali (torus semicircularis or colliculus) are also shown (*sec. VIII*). Under the cerebellum are the cerebellar tracts which envelop the secondary gustatory nucleus (*c*). Granules of the cerebellum are marked *gr.*; those of the valvula, *g*. The bodies of the Purkinje cells of the cerebellum are indicated by dotted outlines. *nuc.com.*, is the commissural nucleus of CAJAL.


tectum opt.
optocoele
sec. VII.
gust. 3.
lobus inferior
gl.
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com. VII
facial lobe
sec. gust. t.
trigemino-bulbaris
sec. VII.
desc. sec. VII.
mucous com.

and are of the same type as in cyprinoids. Their neurites, mingling with the tractus lobo-cerebellaris, pass down to end in the inferior lobe of the same side, essentially as already described for the carp. The ventral portion of this tract and its terminal arborizations are seen in Fig. 37.

The return path in the oblongata by way of the tractus lobo-bulbaris is also essentially as described for the carp.

Section V. Summary and General Conclusions.

In this section a brief summary of the facts as described in the preceding pages is followed by a discussion of some of the morphological considerations growing out of them.

The teleostean fishes generally possess taste buds freely scattered over the mucous surfaces of the mouth, gills and lips. The group of Ostariophysi is characterized by a very great development of this system of sense organs—in the siluroids in the outer skin and barblets and in the cyprinoids both in the outer skin and in still greater degree in the palatal organ within the mouth.

It has previously been shown experimentally that these fishes do in reality taste with their cutaneous taste buds, which are often called terminal buds and which have no relationship whatever with any variety of lateral line organs. Furthermore, while pure cutaneous gustatory stimuli can be localized by the fish, ordinarily both gustatory and tactile stimuli cooperate in the discrimination and localization of food objects.

The distribution and innervation of the organs of taste have been accurately determined for the siluroid fish, Ameiurus, all of them being innervated by the communis system of peripheral nerves. The nerves from the buds in the outer skin enter the brain exclusively by the facialis root ; those from within the mouth by the facialis, glossopharyngeus and vagus roots, chiefly the latter. A special tuberosity of the brain, the lobus vagi, serves in fishes generally as the primary cerebral center for all gustatory nerves. This is greatly enlarged in some cyprinoids to provide for the taste buds in the palatal organ, and in both cyprinoids and siluroids there is another tuberosity de-

veloped, the lobus facialis, which receives all the gustatory nerves from the outer skin.

The purpose of this study is to trace the farther course of these gustatory pathways within the brain and in particular to map out the reflex paths for the various types of gustatory reaction which have been actually observed in the feeding activities of these fishes.

Peripheral gustatory nerve fibers (especially those of the X and IX nerves) enter the brain in company with unspecialized visceral sensory fibers from which they can be distinguished within the brain only with difficulty. This mixed system is spoken of as the communis system of nerves and centers. It is probable that the complete analysis of this complex can be made only by the degeneration method. But the comparative method has enabled us to determine with great probability the chief secondary connections of both types of fibers and so to prepare the way for an accurate determination of the gustatory pathways in the human brain, which are at present almost wholly unknown.

In the cyprinoids and siluroids the primary gustatory centers possess in both the facial and the vagal lobes two types of secondary neurones; (1) small intrinsic neurones (largely of GOLGI'S type II) filling the interior of the lobe, and (2) larger and very highly specialized neurones superficially arranged over the lobes—the chief secondary gustatory neurones.

The intrinsic neurones serve to diffuse incoming stimuli throughout the substance of the lobes and those with longer neurites effect connections with adjacent motor areas, chiefly by way of the substantia reticularis grisea. These connections are probably very largely for unspecialized visceral sensory reflexes, as well as for direct response of the mandibular branchial and palatal musculature (muscles of the visceral system) to gustatory stimulation, and are probably substantially similar in all vertebrates.

The chief gustatory neurones of both vagal and facial lobes give rise to the long paths of secondary connection for distant parts of the brain. Their dendrites receive directly the per-

ipheral gustatory terminals of the first order and their neurites either descend to the inferior secondary gustatory nucleus in the region of the funicular nuclei or ascend to the superior secondary gustatory nucleus in the isthmus. In both cases the path is mainly and perhaps exclusively gustatory in function.

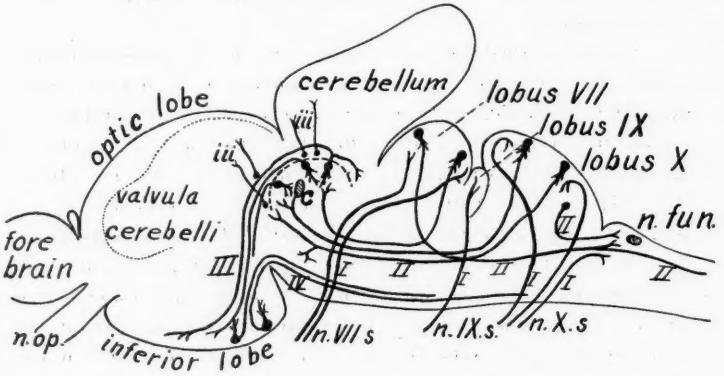

Fig. 38. Diagram of the gustatory paths in the brain of the carp as seen from the side. Only the long paths are shown in this diagram (cf. Fig. 39).

n.VII.s., n.IX.s., and n.X.s., represent the sensory root fibers of the facialis, glossopharyngeus and vagus respectively, or gustatory neurones of the first order (*I*). The secondary tracts, both ascending and descending, are marked *II*. The tertiary path to the inferior lobe is marked *III*; the path to the cerebellum and valvula, *iii*. The return path from the inferior lobe to the motor nuclei of the oblongata (tractus lobo-bulbaris) is marked *IV*. The commissures of the inferior and superior secondary gustatory nuclei are indicated by shaded areas (the latter marked *c*). *n.op.*, the optic nerve. The area marked *n.fun.* includes the funicular nucleus and the inferior secondary gustatory nucleus.

In cyprinoids the gustatory neurones of the smaller type probably share both this function and that of the intrinsic neurones. In no case does a peripheral gustatory neurone connect directly with a peripheral motor neurone. There is always at least one intermediate neurone between them.

The vagal lobes of the larger cyprinoids differ from those of the siluroids, in addition to the points already mentioned, in the following respects: (1) The chief secondary neurones, being exceedingly numerous and crowded in a narrow peripheral

layer, thrust their dendrites inward in a radial direction and there engage the termini of the peripheral neurones of the first order instead of spreading out tangentially among these termini, and the neurite arises from the tip of the dendrite. This ar-

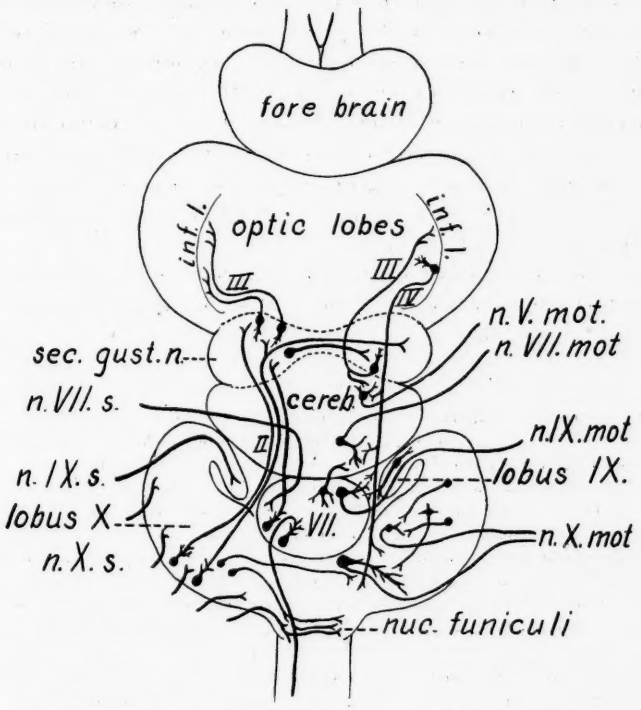

Fig. 39. Diagram of the gustatory paths in the brain of the carp as seen from above. Designations in general as in Fig. 38.

The sensory root fibers and long sensory tracts are indicated on the left side; the short paths, return path from the inferior lobe and motor root fibers, on the right side. The lines, *inf.l.*, designate the outer margins of the inferior lobes. The dendrites of all the motor nuclei ramify in the substantia reticularis grisea. Two types of motor fibers are indicated in the vagus root (*n.X.mot.*), (1) those from the motor layer of the vagal lobe (above), and (2) those from the nucleus ambiguus (below). The facial lobe is designated, *VII*; the superior secondary gustatory nucleus, *sec.gust.n.* The area designated *nuc.funiculi* contains also the inferior secondary gustatory nucleus.

rangement is probably merely a device for economy of space (cf. Figs. 10 and 30). (2) The deepest cells of the vagal lobe are motor neurones (probably derived phylogenetically from the underlying nucleus ambiguus and related to the dorsal motor nucleus of the vagus of FOREL *et al.*) which supply directly the intrinsic muscles of the palatal organ. These motor cells are not present in recognizable numbers in siluroids or other teleosts—correlated with the absence of the palatal organ. (3) A large proportion of the intrinsic neurones serve as intermediaries between the peripheral termini and the motor layer of the vagal lobe, thus providing for a reflex connection within the lobe between the taste buds on the palatal organ and the intrinsic muscles of that organ.

The main paths of gustatory conduction in these fishes may be summarized as follows (cf. the accompanying schemata, Figs. 38 and 39.)

A. Short Paths.

1. Impulses originating in taste buds on the palatal organ pass by way of the X and IX nerves to the vagal lobe; then through the intrinsic neurones to the motor layer and the intrinsic muscles of the palatal organ (in cyprinoids only).

2. From peripheral termini in both the vagal and facial lobes to the substantia reticularis of the same side via intrinsic neurones, the smaller type of marginal neurones (in cyprinoids) and collaterals of the chief neurones. These neurones of the second order, either directly or through the mediation of tertiary neurones of the substantia reticularis grisea, reach the dendrites of the visceral motor nuclei of the medulla oblongata. This provides a pathway for reflex movements of the lips, barbels, tongue, jaws, gills and pharynx in response to gustatory stimulation.

3. Some of the chief gustatory neurones send their neurites directly across the raphé, probably to end in the substantia reticularis of the opposite side of the oblongata. There is also, of course, indirect connection between the substantia reticularis of the two sides of the body, thus providing for coordinated action of the muscles of both sides.

4. The nucleus intermedius of the vagal lobes and the associated substantia reticularis extend caudad from their lobes to fuse directly with important gustatory centers lying mesially of the funicular nuclei—the inferior secondary gustatory nuclei. These nuclei are connected by the commissura infima HALLERI and the commissural nucleus of CAJAL is a specialized part of this gustatory center. These nuclei are very intimately related to the funicular nuclei and thus afford a mechanism of correlation between gustatory and tactile impressions.

B. Long Paths.

5. The descending secondary gustatory tract arises from the chief gustatory cells of the facial lobe mainly and terminates partly in the inferior secondary gustatory nucleus and a smaller part lower down in the spinal cord. This puts the taste buds in the outer skin into very direct relations with the trunk musculature and so provides for the body movements necessary to turn and seize food after its detection by contact with cutaneous taste buds. This inferior nucleus, as stated above, is connected by a rich fibrous plexus with the funicular nucleus, which is the primary tactile coordination center for the skin of the head and trunk. Thus the cutaneous gustatory and tactile impressions may be brought into relation, as required by the physiological evidence that these senses cooperate in the localization of food objects.

6. The ascending secondary gustatory tract arises from the chief secondary neurones of both vagal and facial lobes and terminates in the superior secondary gustatory nucleus located in the lateral wall of the isthmus (the "Rindenknoten" of MAYSER). It ends chiefly on the same side, but a part of its fibers cross through the commissure of the secondary nuclei to end in the opposite nucleus.

The superior and inferior secondary gustatory nuclei are both specializations of the substantia reticularis grisea. The superior nucleus is especially intimately connected with the motor V nucleus, partly directly and partly through another specialized area termed the substantia reticularis grisea trigemini. It also has connections cephalad with the region of the eye-muscle nuclei and the nucleus of the fasciculus longitudinalis medialis, thus putting the gustatory system into physiological relation with the somatic motor centers. There is also probably an important connection between the superior nucleus and the cerebellum and valvula cerebelli by way of the nucleus lateralis valvulae. These important mesencephalic and cerebellar connections merit much more thorough study.

7. The chief tertiary gustatory tract arises from cells in the cortical layer of the secondary nucleus, whose dendrites receive the terminal arborizations of the secondary fibers. This tract is heavily medullated and mingles with the tractus lobo-cerebellaris (EDINGER) and other vertical tracts connecting with the cerebellum, so that it is difficult to follow it separately. GOLGI impregnations show that its fibers pass ventrad and slightly cephalad to arborize widely throughout the lateral lobule of the inferior lobe (hypoaria, C. L. HERRICK) along with others from the forebrain, tectum, etc. This appears to be the chief center for the correlation of olfactory and other higher senses.

8. The return path for all of these sensory activities of the inferior lobe is the tractus lobo-bulbaris, the dendrites of whose cells of origin ramify widely among the gustatory and other terminals just mentioned. This tract (MAYSER'S "Nervenfaser-bundel x") passes into the oblongata mesially of and partly enclosed by the ascending secondary gustatory tract and along the lateral border of the substantia reticularis grisea, within which its fibers gradually diffuse themselves. Through the medium of this reticular area the descending impulses from the inferior lobe come into relation with the peripheral motor neurones of the oblongata and probably also of the spinal cord, thus providing for the most complex reflexes of which the fish is capable.

TABLE OF THE GUSTATORY PATHS IN FISHES.

A. PERIPHERAL NEURONES—GUSTATORY NEURONES OF THE FIRST ORDER.

I. Radix communis facialis.

II. Radix communis glossopharyngei.

III. Radix communis vagi.

These radices contain unspecialized splanchnic fibers in addition to gustatory fibers. In their intra-medullary courses they unite to form the fasciculus communis of the Ichthyopsida, or the fasciculus solitarius of birds and mammals. In some animals the secondary gustatory fibers are also in part represented in this tract.

B. NUCLEUS GUSTUS PRIMUS.

The communis roots terminate in a medullary center which may be termed the primary communis center. That portion of this center which receives the gustatory component of these roots is the primary gustatory nucleus. It may be single, but in the fishes described in this paper is double.

I. Lobus Vagi.

1. Layer of root fibers.
2. Layer of secondary neurones.
   1) Chief secondary neurones.
   2) Intrinsic secondary neurones.
3. Layer of secondary gustatory tracts.
4. Layer of motor neurones.
5. Ependyma.

These layers occur as above only in some cyprinoids. In place of the 4th layer in siluroids is the nucleus intermedlus vagi, and in these fishes the chief gustatory neurones are arranged in dorsal and lateral groups with somewhat different secondary connections.

II. Lobus facialis (=tuberculum impar=lobus trigemini, MAYSER).

1. Chief secondary neurones.
2. Intrinsic secondary neurones.
3. Nucleus intermedius facialis.

III. Lobus glossopharyngei (in cyprinoids only).

C. TRACTUS GUSTUS SECUNDUS DESCENDENS.

1. Pars facialis (distinct only in cyprinoids and siluroids).
2. Pars vagi (part of the spinal portion of the fasciculus solitarius in mammals).

D. TRACTUS GUSTUS SECUNDUS ASCENDENS (central gustatory tract = "sekundäre Vagus-Trigeminusbahn," MAYSER).

1. Pars facialis (in cyprinoids and siluroids only).
2. Pars vagi.

E. NUCLEUS GUSTUS SECUNDUS INFERIOR.

F. NUCLEUS GUSTUS SECUNDUS SUPERIOR (central gustatory nucleus = "Rindenknoten," MAYSER=secondary vagus nucleus, JOHNSTON).

1. Commissure of secondary gustatory nuclei.
2. Intrinsic neurones (mainly commissural?).

3. Chief tertiary gustatory neurones.

G. TRACTUS GUSTUS TERTIUS.

1. Ad lobum inferiorem.
2. Ad cerebellum.
3. Ad mesencephalon.
4. Ad substantiam reticularem.

A detailed discussion of the *mammalian homologies* of the tracts and nuclei enumerated in the preceding table is as yet premature. Much further work on the intermediate types remains to be done before such comparisons can have much value except as suggestions for further research.

In the human body the lingual branch of the glossopharyngeal nerve (from taste buds at the base of the tongue) undoubtedly corresponds to a portion of the pre-trematic branch of the same nerve in fishes. The course of the peripheral gustatory nerve from the taste buds at the tip of the tongue is still disputed, though the evidence is rapidly accumulating that this course is via the lingual nerve, chorda tympani and portio intermedia of WRISBERG into the fasciculus solitarius. The homologies of the chorda tympani have given comparative anatomists a world of trouble. If the gustatory component of the chorda in man supplies taste buds on the tip of the tongue, it is obvious that in the fishes there can be no strictly homologous nerve, for there is no fleshy tongue in fishes. From what branch of the piscine facial nerve the mammalian chorda tympani has been specialized is uncertain—possibly from none of them.

The identification of the fasciculus communis of amphibia with the fasciculus solitarius of mammals was a very important step in advance. In the teleosts the case is much more complicated and difficult of correlation. But the descriptions of CAJAL ('96, p. 43) permit comparisons which are very close in all fundamental respects. In the new-born mouse there is a single sensory root for the vagus and glossopharyngeus and a single terminal nucleus which is the grey substance associated with the fasciculus solitarius. In addition to the dorsal nucleus of KÖLLIKER, which is a specialized portion of this substance, there is another and more important specialization from it in the

region of the funicular nuclei. Here is a commissure which corresponds to the commissura infima HALLERI of teleosts and a commissural nucleus which is also present in fishes and which is closely related to the inferior secondary gustatory nucleus of my descriptions. In the mouse the greater part of the primary sensory root fibers of the IX and X nerves appears to end in this nucleus; in the fishes a very small part, while the greater part of the fibers end in the vagal lobe whose sensory portion is homologous with the dorsal sensory nucleus of KÖLLIKER. The commissural nucleus of CAJAL, as a primary end-station for the spinal root of the vagus, is homologous with the terminal nucleus of the descending vagus root fibers associated with the inferior secondary gustatory nucleus. The latter nucleus is not represented in CAJAL's descriptions, though I venture the prediction that further study of the mammals will show that it too is represented in the commissural nucleus. CAJAL finds that the neurites of the cells of the commissural nucleus enter the lemniscus along with secondary tracts from the funicular nuclei (secondary tactile path), and here again the teleostean and mammalian relations are closely parallel.

HIS has shown that the fasciculus solitarius, when first apparent in the human embryo, lies, like the spinal V, superficially on the lateral border of the oblongata and its deeper adult position is due to the overgrowth of structures from the "Rautenlippe." In teleosts it lies still deeper, as close to the median line as possible. This may be explained by the fact that the fasciculus solitarius as a visceral sensory tract is more ancient than the specialized somatic sensory enlargement (tuberculum acusticum) of this part of the oblongata. The communis VII + IX (= fasc. communis) was therefore passively crowded inward from the primitive superficial position by the over-growth of the tuberculum acusticum (and later by the "Rautenlippe" for the olive) and prevented from passing ventrally by the great ventro-lateral tracts and the secondary mechanism for the tuberculum acusticum. The spinal V tract, however, being organically connected with the somatic sensory centers here develop-

ed, retained its superficial position with reference to them. In passing from the fishes to the mammals the fasciculus solitarius has been crowded again somewhat laterally on account of the further development of median structures.

The short gustatory paths between the primary centers and the motor nuclei of the oblongata by way of the substantia reticularis are essentially the same in the fishes and mammals.

The homology of the nucleus ambiguus of fishes and mammals is not open to question. FOREL in 1891 showed that the so-called chief or dorsal sensory nucleus of the IX and X nerves of mammals is in reality a motor nucleus of origin for these nerves and much evidence in confirmation of this view has since been published. The motor layer of the vagal lobe of cyprinoids corresponds in position exactly with this nucleus and is probably in a broad way homologous with it, though of course the homology is not exact.

The long ascending secondary tracts from the vagal and facial lobes (central gustatory path, or tractus secundus ascendens) has not been identfied in any vertebrates save the fishes, though it has long been in the minds of several neurologists that the homologies of this tract are to be sought in the lateral cerebellar tract of FLECHSIG (tractus spino-cerebellaris dorsalis, EDINGER). These fibers are known to arise from the cells of CLARKE'S column (supposed to be a visceral sensory center) and to enter the vermis cerebelli by way of the restiform body of the same side. Dorsally of the ventricle they cross to the opposite side and the whole arrangement strongly suggests a survival of a primitive secondary tract from the visceral sensory center of the spinal cord to the isthmus, to which in fishes the strong secondary gustatory tracts arising in the oblongata are added. This suggestion, however, cannot be taken seriously until we have much more exact knowledge of the superior connections of these fibers in the mammals and of the comparative anatomy of the structures at the base of the vermis cerebelli.

The morphological relations of the secondary gustatory tract and nucleus are clearly defined. The tract represents a specialization of the substantia reticularis alba and the nucleus

a similar derivative of the substantia reticularis grisea. The lemniscus (fasciculus lateralis) of these fishes represents a similar specialized somatic sensory path from the primary tactile and acustico-lateral centers to the nucleus lateralis mesencephali (torus semicircularis, or colliculus), whose fibers cross in the ventral commissure of the oblongata. This special splanchnic (gustatory) path appears to have been differentiated later in the phylogeny than the secondary somatic path. Hence its superficial position, coenogenetic structures of the brain being generally added external to palingenetic structures. The crossing of the visceral path within its terminal nucleus instead of at its origin in the oblongata is perhaps due to the same cause, the primitive undifferentiated visceral path having been uncrossed or diffusely crossed because these sensations are not localized ordinarily. The *unspecialized* secondary visceral path doubtless is as primitive as the unspecialized somatic path and probably was originally a diffuse connection by short fibers in the substantia reticularis (crossed or uncrossed). But the ascending gustatory tract (specialized visceral) as a well defined conduction path is quite certainly more recent. This does not affect the conclusion to which we were led above that the visceral root fibers (fasciculus communis) are older than the *special* somatic centers in the tuberculum acusticum.

The topography of the oblongata suggests that upon the basis of the unspecialized centers the ascending secondary paths for the specialized systems were added in the following order,—first, the somatic sensory, or lateralis system for orientation and equilibrium, and, second, the gustatory. The latter is a strictly visceral system except that in some fishes important somatic secondary connections appear sporadically in correlation with the appearance of taste buds in the outer skin.

The mammalian homologies of the superior secondary gustatory nucleus cannot be determined until its relations to neighboring structures are much more fully known. STIEDA's original designation, "Uebergangsganglion," apparently included much more than the secondary gustatory center, which is probably coextensive with MAYSER's narrower term, "Rindenknot-

en." MAYSER ('82, p. 334) identifies the "Uebergangsganglion" with the corpus quadrigeminum posterius of FRITSCH ('78). From the latter's figures, I infer that he included under this term the structures adjacent to the secondary gustatory nucleus as far as cephalad as my nucleus lateralis valvulae. The latter nucleus is apparently included in the "cells of the superior and internal regions of the torus semicircularis" of CATOIS ('01, p. 133). CATOIS' "cells of the external region of the torus" constitute the nucleus lateralis mesencephali of EDINGER. EDINGER states that the "Uebergangsganglion" of STIEDA (sekundäre Vaguskern) is homologous with his ganglion isthmi ('96, p. 94 and '03, p. 75). He also identifies ('04, p. 194) the ganglion isthmi with the nucleus tegmenti dorsalis of VON GUDDEN and thinks it probably is the same as BECHTEREW'S corpus parabigeminum. EDINGER adds ('04, p. 267) that the ganglion isthmi of lower vertebrates receives the median root of the optic nerve and gives rise to centrifugal fibers for the retina. His account make it probable that his ganglion isthmi sould be identified with my nucleus lateralis valvulae rather than with the "Uebergangsganglion" as a whole. Though I have not traced the fibers of the mesial optic root so far caudad as this, yet the connection with the post-optic commissure, referred to by EDINGER, is very plain, and the tract running from the cephalic end of the n. lateralis valvulae to the oculomotor nuclei lends probability to the belief that the n. lateralis valvulae is in part a path for oculo-motor reflexes and probably also somatic motor reflexes via the fasciculus longtitudinalis, of optic, gustatory and perhaps olfactory origin. My n. lateralis valvulae is apparently included in the "ganglio subcerebelloso" described ('94, p. 96) and figured ('94 a, Fig. 4, p. 203) by CAJAL. His figure shows the cells provided with a single thick unbranched dendrite which comes into relation with collaterals from the ventral longitudinal tracts of the mid-brain.

The only conclusion at present possible is that the "Uebergangsganglion" is a very complex structure, devoted largely to gustatory reflexes and coordinations of several sorts, and

doubtless with other important connections as yet imperfectly known.

While these pages are passing through the press the excellent paper by GOLDSTEIN (Untersuchungen über das Vorderhirn und Zwischenhirn einiger Knochenfische, nebst einigen Beiträgen über Mittlehirn und Kleinhirn derselben. *Arch. f. mikr. Anat.*, LXVI, 2, 1905, pp. 135-220), on the brains of teleosts has come to hand. While GOLDSTEIN'S detailed examination did not extend back into the region of the gustatory centers, yet I am pleased to note that he found and figured the tertiary path to the inferior lobes, though naturally without being able to give its functional interpretation. It has been assumed by some authors that the ganglion isthmi of EDINGER is the same as the "Rindenknoten" of MAYSER (my nucleus gustus secundus superior). GOLDSTEIN, however, terms the latter "nucleus lateralis cerebelli" and the cells which he designates as ganglion isthmi are clearly shown by his figures to be the cortical layer of tertiary gustatory neurones surroung the "Rindenknoten" as I have described them in the preceding pages. GOLDSTEIN'S tractus isthmo-hypothalamicus, then, is my tertiary gustatory path to the inferior lobe. It is apparently another portion of this tertiary gustatory path which he shows in text-figure 21 (p. 206) entering the tr. cerebello-thalami from the dorsal part of the nucleus lateralis cerebelli.

There remain to be considered the *morphological relations of the gustatory system* as a whole to the other functional systems of the brain. The intimate association of gustatory fibers with those of general visceral sensation, both in the peripheral and the central nervous system, strongly suggests that the gustatory system has been specialized from this primitive source; but it must be admitted that the evidence thus far produced, while very suggestive, can hardly be called demonstrative. A comparison of the gustatory system with the "visceral sensory system" cannot be expected to yield very important results so long as the latter system remains so imperfectly understood. There is a strong demand for an analysis of the visceral nerves and for a clear understanding of the relations (both anatomical and physiological) of their various kinds with certain systems commonly classified with the somatic sensory group, such as the nerves of muscle and joint, thermal and pain (?) sensations.

Whatever the phylogenetic origin of the gustatory system, it is clear that it is confined to the cranial nerves and that in the lowliest vertebrates it is represented in at least three of these nerves. The primary terminal center does not corres-

pond topographically with the dorsal horn of the spinal cord, but with the region of CLARKE's column. In the present state of our knowledge, no precise comparisons are possible between the gustatory secondary connections and those of the visceral centers of the spinal cord. And in the brain, where our knowledge of the connections of the nerves is more exact, there is no close resemblance between the secondary gustatory and any other secondary sensory system.

The acustico-lateral and tactile systems have been shown to be intimately related and their secondary tracts in fishes are, in a general way at least, known, crossing immediately in the ventral commissure and ascending in the lemniscus (fasciculus lateralis) to the opposite mesencephalon. Clearly there is no close resemblance here with the gustatory connections and it is difficult to conceive how either form could have been derived from the other.

Given a primitive elongated gustatory center in the oblongata, like that associated with the fasciculus communis of the amphibia, and the development of all types of primary gustatory centers known among fishes can be easily understood by simple hypertrophy of different parts of the system. We have seen in the preceding descriptions that the secondary gustatory connections are in almost all cases through the substantia reticularis grisea or derivatives from it. This applies both to the short connections and to those by way of the superior and inferior secondary nuclei. In the two latter cases the connection is partly on the same side and partly on the opposite side through a commissure.

The superior secondary nucleus is clearly adapted to serve the higher gustatory reflexes, and various coordinations, chiefly with smell and sight. The connection with the valvula cerebelli and cerebellum is very perplexing. There is a suggestion in certain comparative anatomical facts that the valvula cerebelli of teleosts (or at least its lateral lobes which are broadly confluent with the nucleus lateralis) has been differentiated in connection with the secondary gustatory nucleus. The valvula is largest in those teleosts which have the most highly developed

gustatory systems, and it was noticed by MAYSER ('82, p. 325) that the cephalic part of the "Uebergangsganglion" (including my nucleus lateralis valvulae) varies in size with the valvula cerebelli, while the caudal part (which corresponds in part with our substantia reticularis grisea trigemini) varies with the size of the secondary gustatory tracts. In Mormyrus, where the lateral lobes of the valvula attain so enormous size as to expand upwards and laterally in mushroom shape and overlap the whole brain, SANDERS ('83) describes also a considerably enlarged and modified tuberculum impar and vagal lobes. Since the other parts of this brain are of the typical teleostean type, save for the reduction of the visual apparatus and inferior lobes, it appears probable that the lateral lobes of the valvula are related with the gustatory reflexes.

The chief connections of the cerebellum are with centers commonly regarded as of the somatic sensory type—tactile, acustico-lateral, visual. This strengthens the current view that this organ is concerned with the regulation of somatic movements, or reactions of the body to external stimuli as distinguished from visceral reactions to internal stimuli. A gustatory cerebellar connection would seem, therefore, very anomalous. And so it would be in an ordinary vertebrate, if our present functional analysis is proceeding along true lines. But we have seen above that the fishes here under consideration, unlike most other vertebrates, make somatic movements in response to cutaneous gustatory stimulation in their ordinary feeding reactions. This feature gives an abundant explanation for the cerebellar connections of the secondary gustatory nucleus, by way of the nucleus lateralis valvulae, as well as a possible clue to the morphology and phylogeny of the valvula.

The problem of the relation of taste and smell is of major importance from the points of view of comparative physiology, of phylogeny and of morphology. Why the single chemical sense of some invertebrates should have given rise in the vertebrates to two systems so distinct morphologically as the olfactory and gustatory apparatus has not been explained. A suggestion of a possible genetic connection is manifest in the ac-

companying diagram (Fig. 40) of the morphological relations.

Remembering that the secondary gustatory connections are differentiations from the substantia reticularis grisea (the anomalous position of the superior secondary nucleus being easily explained on mechanical grounds), we find here a natural explanation of the further (tertiary) path to the inferior lobe, for this is also a derivative of the substantia reticularis, crowded for mechanical reasons in the opposite direction from that taken by the secondary gustatory nucleus (cf. JOHNSTON '02 a, p. 100). Turning now to the secondary olfactory connections, the resemblance to those of the sense of taste is striking in fundamentals, in spite of great difference in detail.

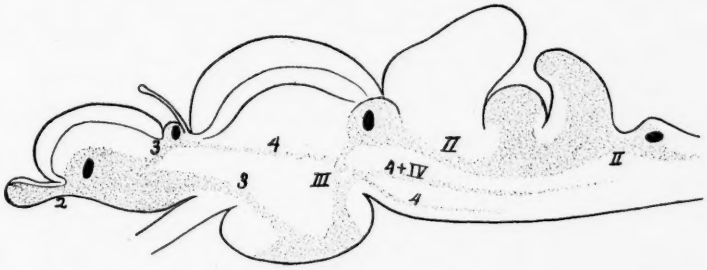

Fig. 40. Diagram showing the relations of the gustatory and olfactory centers in teleosts, as represented by the shaded areas. The black spots represent the position of commissures of secondary or tertiary fibers. 2, 3 and 4 represent the olfactory conduction paths of the second, third and fourth orders respectively. II, III, IV represent the gustatory conduction paths of the second, third and fourth orders respectively. Compare Figs. 38 and 39.

The olfactory bulb, like the vagal lobe, contains a marginal zone of large secondary cells, the mitral cells, with long neurites and with dendrites which receive the endings of the peripheral neurones. The interior of the bulb is filled with minute intrinsic neurones. The secondary center is the area olfactoria of the fore-brain, whose commissure bears the same relation to the secondary tracts as do those of the secondary gustatory nuclei. The main tertiary tract passes, as before, to the inferior lobe, which is, in fishes, the central correlation station for all sensory impressions. The return path from the inferior lobe to

the epistriatum in teleosts is a prophesy of the evolution of the cortex cerebri in the later phylogeny. The olfactory and gustatory tertiary tracts end together throughout the inferior lobe and they have a common descending conduction path, the tractus lobo-bulbaris. In addition to this ventral olfactory path, there is the dorsal tertiary tract from the fore-brain to the habenula and its descending path of the fourth order, MEYNERT'S fasciculus retroflexus. This path offers opportunity for somatic sensory (including optic) and somatic motor connections analogous to those provided for the sense of taste in the inferior secondary nucleus.

If the olfacto-gustatory connections of the human body are at all similar to these of fishes, this relation offers a possible anatomical correlate of the familiar fact of experience that subjectively we distriminate tastes and smells only imperfectly, in many cases not at all, without the aid of collateral physiological experimentation to determine which organ receives the stimulus.

It is freely granted that these comparisons are, in the present state of our knowledge, rather fanciful. They are offered merely as the first practicable working hypothesis for a correlation of the olfactory with the other sensory mechanisms. If the anterior end of the primary nerve tube lies in the region of the preoptic recess, as seems to be now commonly assumed, the peculiar relations of the rhinencephalon are to be explained as due to the suppression of the most anterior sensory and motor centers of other systems, leaving the olfactory apparatus free to develop without constraint.

The most striking difference noticeable in the diagram between the centers for taste and smell is the apparently ventral position of the primary and secondary olfactory centers as contrasted with the dorsal centers for taste. But if the anterior end of the brain tube lies near the preoptic recess in the lamina terminalis, this difficulty disappears; for all structures in front of this point must have been developed from the dorsal wall of the brain tube. That is, the secondary fore-brain, including the entire rhinencephalon, is a dorsal structure.

Our conclusion, then, is that the morphological relations

expressed in Fig. 40 strongly suggest that the central reflex mechanisms of taste and smell have had a common phylogenetic origin and that they have been from the first quite independent of the so-called somatic sensory centers.

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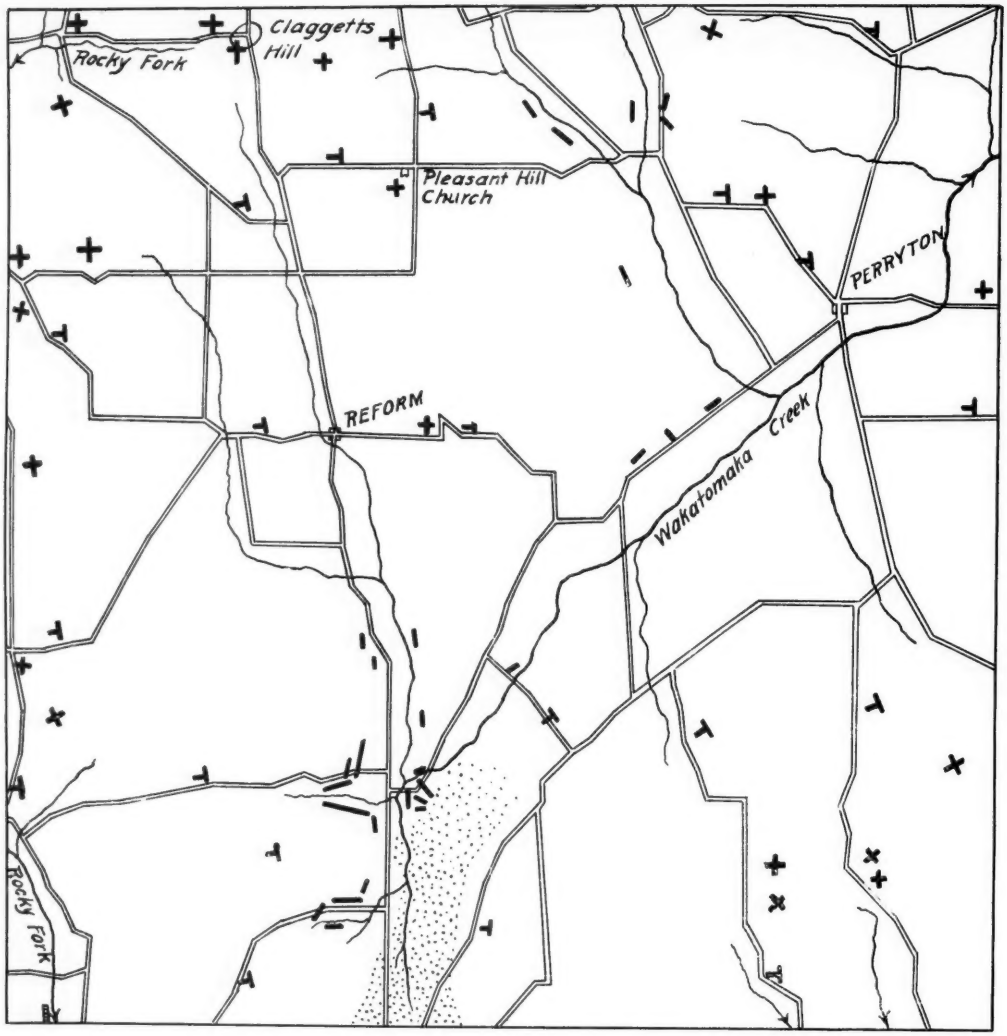

PERRY TOWNSHIP, LICKING COUNTY, OHIO.

0 ½ 1 MILE

PLATE I.

BLACK HAND CONGLOMERATE

DRIFT AREA

SHARON CONGLOMERATE

LOGAN FORMATION

CUYAHOGA FORMATION

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